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STUDIES OF CERTAIN COASTAL SAND DUNE PLANTS OF SOUTHERN CALIFORNIA

By

EDITH A. PURER
San Diego, California

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STUDIES OF CERTAIN COASTAL SAND DUNE PLANTS OF SOUTHERN CALIFORNIA[1]

INTRODUCTION

The published literature on the vegetation of the coastal sand dunes of southern California is concerned with taxonomic matters and to a much lesser degree with successional relations. The present investigation deals with the autecology of some representative species of plants of this area. In addition certain environmental conditions have been studied, in order to determine under what general ranges of these important conditions this particular sand dune vegetation exists.

METHOD OF PROCEDURE

After a general survey of the sand dune areas of southern California, eleven representative species[2] were chosen, namely: *Abronia maritima* Nutt.,[3] *Abronia umbellata* Lam., *Atriplex leucophylla* Dietr., *Convolvulus soldanella* L., *Ericameria ericoides* (Less.) Jepson, *Eriogonum parvifolium* Sm., *Franseria bipinnatifida* Nutt., *Lupinus chamissonis* Esch., *Mesembryanthemum aequilaterale* Haw., *Oenothera cheiranthifolia* Hornem. var. *suffruticosa* Wats. (Munz, 1928), *Rhus integrifolia* B. and W.

The gross morphology of the roots, stems, leaves, flowers and fruits was investigated, and the subterranean and the aerial portions of the plant were measured and charted. Leaves, stems and roots were sectioned and variously stained for consideration of their anatomical structure. Certain habitat conditions under which the species grew were measured for fifty-six consecutive weeks.

LITERATURE

Literature relating to the coastal sand dune areas of California is scanty. Reforestation problems received the attention of several individuals. Cooper (1922) refers to the development of coastal dunes in a brief paragraph and he has a comprehensive study of this strand vegetation in progress (Carnegie Institution Yearbooks, 1919, 1920, 1922). A quadrat study of an area in Los Angeles County was made by Couch (1914) while a floristic investigation was undertaken by Olsson-Seffer (1910) along the California coast. Abrams (1917) and Jepson (1925) have given in their manuals descriptions and distributions of sand dune species.

[2] Hereafter when only the genus name is stated the particular species given below is implied.
[3] Jepson (1925) was followed in naming plants unless otherwise stated.

In other regions several comparative studies of sand dune plants have been made. Chrysler (1904) examining the leaf anatomy of plants growing on the Atlantic coast and on the shore of Lake Michigan found that:

(1) Plants growing in the maritime situation have thicker leaves than the same species growing inland, and (2) This increase in thickness of the leaf is always due, at least in part, to an increase in thickness of the palisade layer, and also (3) In some cases the number of palisade layers is increased in the maritime situation.

Starr (1912) makes the following statement:

Plants generally growing in mesophytic situations, when found also on the dunes, show the following modifications; *of the leaf,* increased thickness, decrease in depth and increase in surface-extent of the epidermal cells, increase in thickness of the outer wall of the epidermis and of the cuticle accompanied by ridging, increase in palisade, in hairs, in conductive and mechanical tissues; *of the stem,* decrease in the length of internodes, increase in the number of vessels and in the area of their cross-sections, giving greater conductive space, increase in thickness of the walls of vessels and of the fibers accompanied by decrease in lumen of fibers, giving more wood, increase in the number of rings in stems of a given size, showing slowness of growth, increase in mechanical tissues outside the wood, and increase in cork.

Harshberger found a number of modifications in the strand plants of the New Jersey coast (1909) and the sand dune plants of Bermuda (1908). An anatomical investigation of beach vegetation in the Philippines, to which references will be made later, was made by Kienholz (1926).

Waterman (1919)) states in his summary of "Development of root systems under dune conditions" that

These reactions are specific and hereditary, and may reflect the conditions under which the ancestral plants grew. They must be regarded as of great importance in the choosing of species for introduction into conditions where the humus content is uneven.

THE SAND DUNES

LOCATIONS AND THEIR EXTENT

Several reconnaissance trips were made along the California and Oregon coasts from a point a short distance south of Descanso, Baja California, to Florence, Oregon. In southern California a long stretch of small dunes extends from Imperial Beach to Coronado in San Diego County. Holmes (1918) describes the coastal beach and dune sand of San Diego as a narrow strip bordering the ocean, rarely or never exceeding one-eighth mile in width and in places too narrow to map. The most striking development is the long sandy bar that partly encircles San Diego Bay. From there to El Segundo, Los Angeles County, there are merely occasional patches of dunes. Dunes,

however, are well developed at El Segundo. Not again until the northern limit of Santa Barbara County is reached, do large dunes appear.

The areas vary in size from a few acres to a number of square miles, and they may be continuous with the strand or superimposed upon bluffs. Some dune localities are separated from the mainland by bays, as for example, the Silver Strand in San Diego County, while others form a part of the mainland as at Guadalupe. Some of the regions are almost as low as the strand, while in other sections, usually farther from the ocean, the dunes may be over 100 feet in height, with troughs of actively blowing sand between them. Still farther north on the coast of California, and also of Oregon, large dune areas are active.

AREAS FOR INVESTIGATION

Two areas in southern California were chosen for intensive study, namely: El Segundo in Los Angeles County, and the Silver Strand in San Diego County. These regions, some 130 miles apart, present not only the largest stretches of dunes in the southern part of the state, but are also representative of other dune areas along the coast of southern California and show a diversification of vegetation from early stages to late development.

CHARACTER

The sand dunes of California present one of the most dynamic of plant habitats. These regions, as in the case of the Lake Michigan dune studied by Cowles (1899), exhibit a number of distinct developmental stages. Among these the strand or beach at Pismo is notable, while at Guadalupe low fore-dunes are well developed just back of the strand. Moving dunes, a dune complex, and open stretches of sand of great instability and bearing little vegetation, occur at Hauser, Oregon. Near Monterey stabilization is well exemplified, vegetation approximating the climax of that region covering many old dunes. Various stages are exhibited at most of the dune areas.

These sand dunes are inhabited by a rather large number of plant species, over 100 being found on the Silver Strand and El Segundo areas. Growth-forms represented are perennial shrubs, including several species which may become trees elsewhere but are shrubs in the dunes; suffrutescent shrubs; evergreen perennial herbs with aerial portions which die annually; biennials; and annuals. There are species typical of the sand dunes, invaders from other surrounding communities, and ruderals. Pioneers in bare areas are those which are commonly sand dune species, while in later stages of the succession both sand dune species and others become components of the vegetation. About the edges of stabilized dunes ruderals compete with dune plants.

A portion of the vegetation has been disturbed both at El Segundo and at the Silver Strand, due to the construction of a highway and a railroad through the entire length of each area, interfering with succession and introducing ruderals.

Table 1 gives in a general way the coastal distribution of the eleven species studied. This has been ascertained through personal collections and the collating of range data accompanying specimens in the Dudley Herbarium, Stanford University, the herbarium of the California Academy of Sciences, San Francisco, and that of the University of California, in Berkeley.

ORIGIN

The sand dunes of coastal California are of recent geologic origin. Concerning San Diego County, Wiggins (1929) states:

Along the immediate coast line the San Diego Formation is covered by a thin deposit of marine, littoral sand and silt, which constitutes the San Pedro Formation of the Pleistocene.

The beach deposits of Pliocene origin range from zero to fifty feet in depth. A lateral current passing southward along Point Loma, in San Diego County, and eddying below it, is the cause of the sand deposit on the Silver Strand.

As reported by Cooper (1927), the country adjacent to Monterey Bay and south of the Salinas River, covered by a complex of ancient dunes, is related to that period of uplift which characterized a portion of Pleistocene time.

The sand dunes are being built up by wind action from sand brought to the edge of the water by the action of the waves. Reed (1930) in examining sand at Playa del Rey, immediately north of El Segundo, found the sands derived from old rocks of the Santa Monica Mountains farther to the north.

TABLE 1. Coastal distribution of the 11 species.

States and Counties	Abronia maritima	Abronia umbellata	Atriplex	Convolvulus	Ericameria	Eriogonum	Franseria	Lupinus	Mesembry-anthemum	Oenothera	Rhus
Washington	.	x[4]	.	x	.	.	x	.	.	.	.
Oregon	.	x	.	x	.	.	x	.	x	.	.
California											
Del Norte	.	x	.	.	.	.	.	.	.	.	.
Humboldt	.	x	x	x	.	.	x	.	x	.	.
Mendocino	.	x	.	x	.	.	x	.	.	.	.
Sonoma	.	x	.	.	x	x	.	x	.	.	.
Marin	.	x	.	.	.	.	.	x	.	.	.
San Francisco	.	x	.	x	x	.	x	x	x	.	x
San Mateo	.	x	x	x	.	.	x	.	.	.	.
Santa Cruz	.	x	x	x	x	.	x	x	.	.	.
Monterey	.	x	x	x	x	x	x	x	x	.	.
San Luis Obispo	x	x	x	.	x	x	x	x	x	.	.
Santa Barbara	x	x	x	x	x	x	x	x	x	x	x
Ventura	x	x	x	x	.	x	.	.	x	x	x
Los Angeles	x	x	x	x	x	x	x	x	x	x	x
Orange	x	x	x	x	.	x	x	.	x	x	x
San Diego	x	x	x	x	x[5]	x	x	.	x	x	x
Baja California	.	.	x	.	.	.	x	.	x	x	x

[4]x—Species present.   [5]Collected in 1878.

ENVIRONMENTAL CONDITIONS

Plants are affected by both the atmospheric and the soil conditions under which they grow. Data concerning these factors were obtained for air temperature, precipitation, humidity, light, wind, soil moisture, soil character, soil temperature, and certain biotic factors.

STATIONS

For meteorological data on the two sand dune areas the San Diego and Los Angeles records of the Weather Bureau, U. S. D. A., were utilized.

Six stations in distinctive communities of different habitat conditions were maintained for fifty-six consecutive weeks, four at El Segundo and two on the Silver Strand. The following locations were selected: El Segundo, Los Angeles County—(1) On the strand, barely beyond the region of the severest storm waves, in small dunes caused by *Abronia maritima*. (2) On a moving dune, farther removed from the ocean, where there were small mounds of vegetation consisting principally of *Franseria bipinnatifida*. (3) On the lee slope of a stabilized dune. Of all the stations this was at the greatest distance from the ocean, where but little sand movement occurred. The principal species here was *Ericameria ericoides*. (4) In a large thicket of *Rhus integrifolia* which had been growing many years. Silver Strand Beach State Park, San Diego County. (5) On the strand, as at El Segundo, in small dunes caused by *Abronia maritima*. (6) In a large clump of *Rhus integrifolia* on an old stabilized dune near the bay side of the strand.

EVAPORATION

Data on evaporation were secured by means of the standardized Livingston non-absorbing, porous cup atmometers, those of both white and black types being employed. The atmometers were mounted by the Livingston and Thone (1920, 1924) methods. The instruments, in batteries of three white cups at each station, were sunk into the soil for about two-thirds of the height of the reservoir bottles. The evaporating surface of the cups was thus about 25 cm. above the surface of the sand. Weekly readings for each station were made for fifty-six consecutive weeks at the same time of day, never varying by more than an hour. The reservoir bottles were filled from a graduated burette to a file scratch on the neck. All the porous cups were restandardized once every three months, or oftener when deemed necessary (Livingston, 1915). When a restandardized cup was found to possess a new coefficient, the correction of its record was made on the basis that the difference between the new and the old coefficient did not prevail during the first one-third or one-fourth of its intervening record, and the difference was therefore distributed through the remaining two-thirds or three-fourths of that period.

These data (Figs. 1 and 2) show that the highest rates of evaporation occur in the region of the moving dunes and the next lower at the strand locations. In the more stabilized areas represented both by the Rhus stations (4 and 6) and the similarly located Ericameria station (3), the rates are considerably lower. Comparing two of the El Segundo stations it is to be noted that for the most part when the amount of evaporation increases at the Rhus station (4), it increases more rapidly at the Ericameria station (3), while in decreasing at each, it usually decreases slightly less at the Rhus station. Since the evaporation rates were obtained from the white porous cups and the evaporativity (Livingston, 1931) by means of the black porous cups, a fairly accurate idea may be gained of some of the conditions under which the plants live (Figs. 5 and 6).

AIR TEMPERATURE

Graphs of monthly mean maxima and minima (Figs. 3 and 4), were constructed from the records of the Weather Bureau, U. S. D. A., at Los Angeles and San Diego for the three years, January, 1930, to January, 1933. These data are adequate for the two areas in general, but cannot be applied to specific stations in each, where variations in temperature probably occur in dune topography with differing vegetative covers. Consideration of these records shows that there is a gradual rise in the summer with a gradual lowering in the winter months, the total yearly range being small. The range
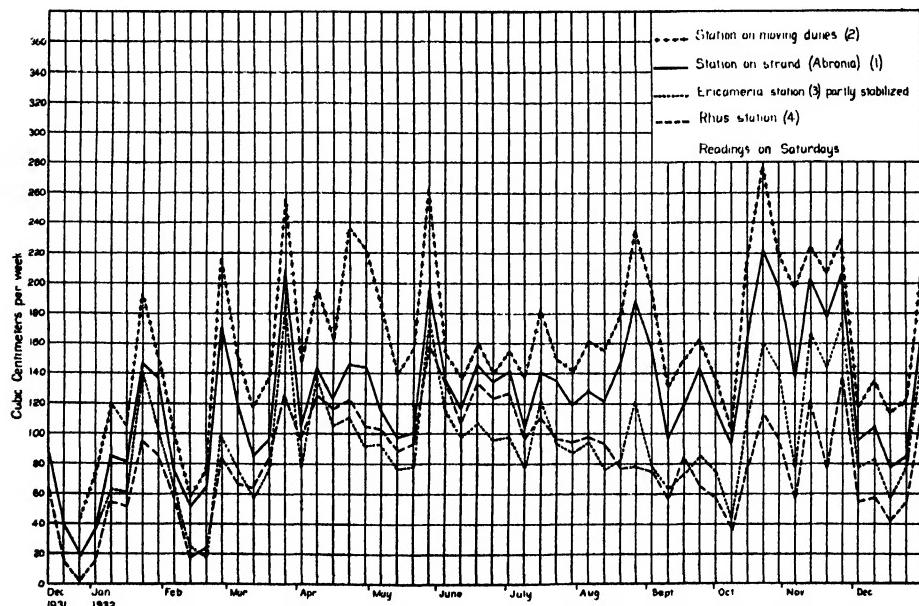
FIG. 1. Weekly evaporation El Segundo, Los Angeles County, December 12, 1931, to January 1, 1933, 56 weeks; Abronia Station (1), moving dune (2), Ericameria (3), and Rhus (4). Livingston white atmometer cups.
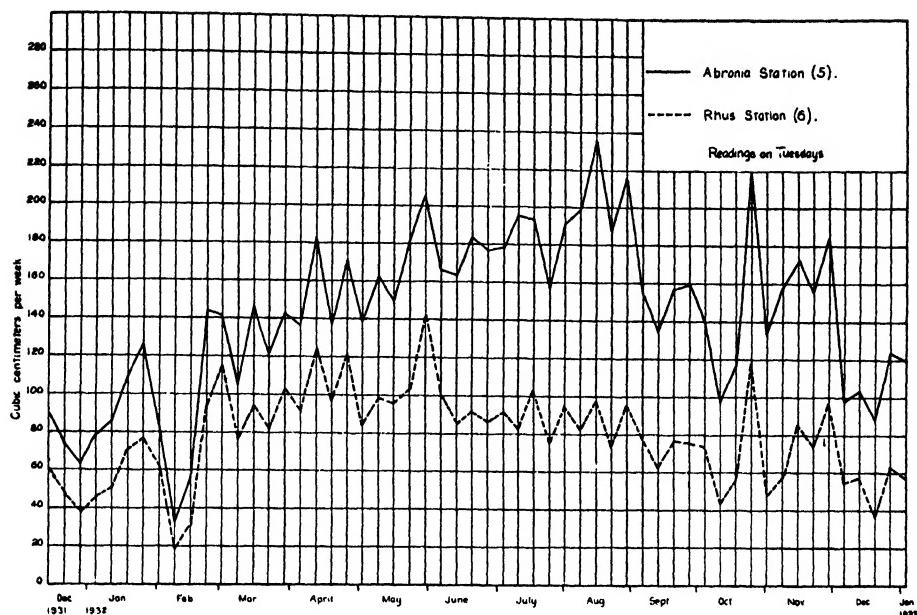
FIG. 2. Weekly evaporation Silver Strand, San Diego County, December 15. 1931 to January 3, 1933, 56 weeks. Abronia station (5), and Rhus station (6). Livingston white atmometer cups.
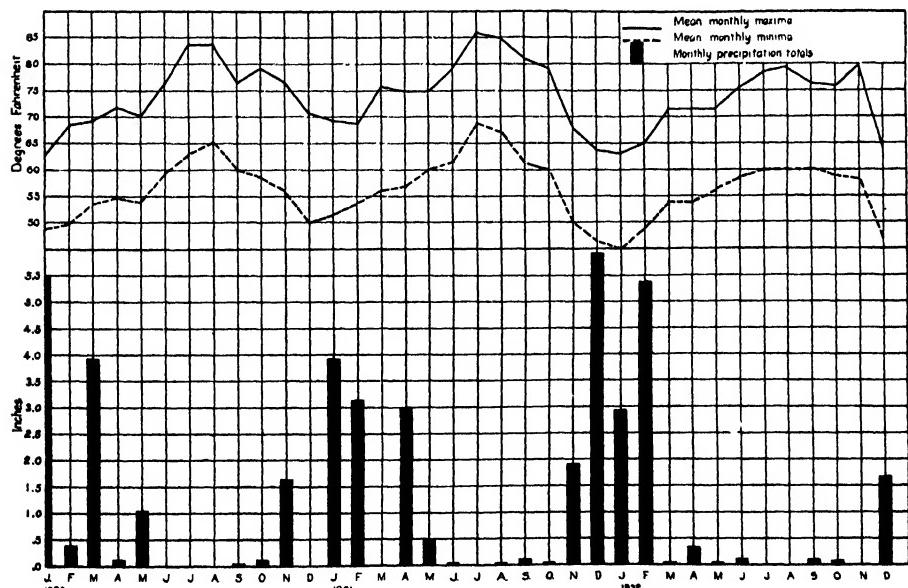
FIG. 3. Temperature and precipitation from January 1, 1930, to January 1, 1933. Weather Bureau, U. S. D. A., Los Angeles.
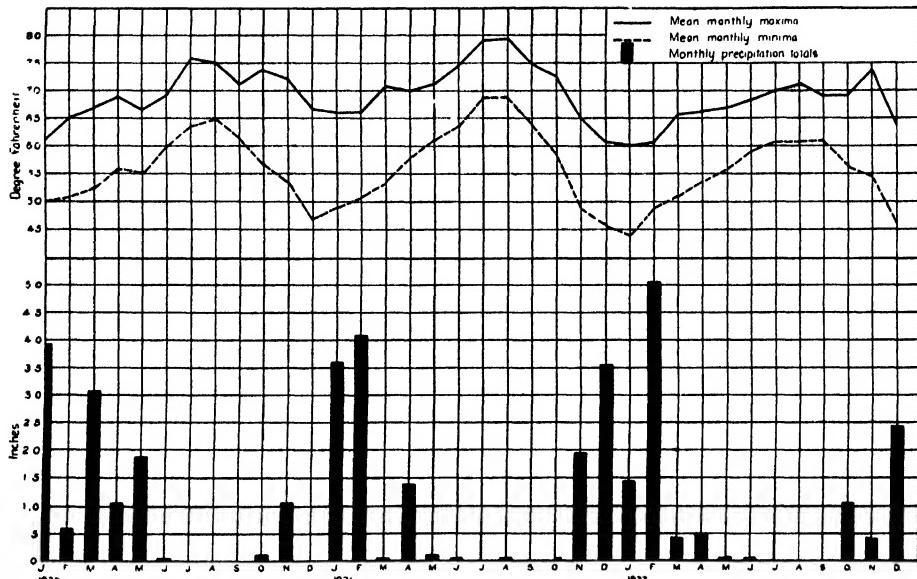
FIG. 4. Temperature and precipitation, from January 1, 1930, to January 1, 1933. Weather Bureau, U. S. D. A., San Diego.

between monthly means of the maxima and the minima was less throughout the year in San Diego than in Los Angeles, at the latter locality the summer mean maxima, for the three months July to September, being approximately 10 degrees greater than in San Diego. It would seem that in general the temperature is favorable for plant growth except when, at very infrequent intervals, it drops below the freezing point.

LIGHT

Maritime dunes are areas of high light intensity for the major portion of a year. In the two areas of investigation the air is clear with no noticeable smoke or soot, the light intensity being diminished, therefore, only by occasional foggy and cloudy weather. The number of days of dense fog, of cloudy and of partly cloudy weather, per month, from January, 1930 to January, 1933, obtained from the records of the Weather Bureau, U. S. D. A., at Los Angeles and San Diego, is given in Table 2. Dense fog occurs infrequently at either station, many months showing a record of but one such day. In San Diego, however, during this three-year period, fog was more frequent during February, October and November. The greater prevalence of fog in San Diego County renders the light over a period of a year less intense than at Los Angeles. Cloudy and partly cloudy days occur more often, appearing at irregular periods in each area.

To obtain a comparison of the radiant energy at some of the dune stations, Livingston black porous cup atmometers (1911) were operated for four

TABLE 2. Number of days of fog and of cloudy weather.[6]

Year and Month	Los Angeles County			San Diego County		
	Partly cloudy	Cloudy	Dense fog	Partly cloudy	Cloudy	Dense fog
1930 January	9	13	0	7	19	0
February	6	3	4	13	7	3
March	10	8	0	8	12	1
April	15	3	1	16	7	0
May	6	6	0	9	10	2
June	8	5	0	7	10	0
July	8	2	0	13	3	0
August	10	1	0	12	6	2
September	14	3	0	17	4	0
October	5	1	1	5	5	4
November	3	4	0	5	4	2
December	5	1	0	5	4	3
1931 January	5	8	0	11	7	1
February	8	8	0	10	10	0
March	9	3	1	6	6	1
April	8	9	0	11	10	0
May	17	4	1	16	6	1
June	14	3	0	9	6	1
July	5	1	1	17	3	1
August	8	3	1	9	6	0
September	5	3	0	8	3	0
October	5	8	1	13	3	1
November	7	7	1	8	9	1
December	10	9	1	10	11	0
1932 January	11	4	0	8	8	0
February	6	11	0	7	13	2
March	7	4	0	10	5	1
April	9	2	1	13	7	1
May	9	8	1	11	10	0
June	6	5	1	16	4	1
July	13	0	0	17	4	0
August	12	2	1	12	8	1
September	17	2	0	19	4	0
October	11	4	1	11	9	6
November	7	2	1	6	6	3
December	7	5	0	6	8	0

[6] Data from Weather Bureau. U.S.D.A.. Los Angeles and San Diego.

months, from September, 1932 to January, 1933, this including the major part of the dry period immediately preceding the rainy season. Two of the atmometers were of the old type, the rest of the new type (Livingston, 1931). They were set up in the El Segundo area at the Ericameria station (3) and the Rhus station (4), and in the San Diego area at the Abronia station (5) and the Rhus station (6) of the Silver Strand. Readings of both the black and the white atmometers were taken weekly during this period (Figs. 5 and 6). A comparison of these data shows that the greatest radiant energy was at the Abronia station (5) on the Silver Strand, while the radiant energy at the other three stations, the Ericameria and Rhus at El Segundo and the Rhus on the Silver Strand, differs but slightly. For the most part, the rates from the white cups at the Abronia and Ericameria stations are higher than those from

the black cups at the two Rhus stations, indicating that the influences affecting evaporation measured by the white cups at the Abronia and Ericameria stations cause greater evaporation than do these same influences, to which is added that of light, measured by the black cups at the Rhus station. This coincides with the fact that Abronia as a pioneer exists under xeric conditions, Ericameria, farther along in the succession, exists under less xeric conditions, and that Rhus represents one of the later stages in the succession when conditions have proceeded farther toward mesophytism.

Most sand dune areas are characterized by exposure to light of high intensity. This is especially the case along the strand and in the moving dunes. Besides illumination from above, there must also be taken into account reflected and diffused light. The light-colored sand, which characterizes the dunes because of the generally sparse vegetation, greatly promotes light-diffusion. The reflection of light by the water and by the foam-crested
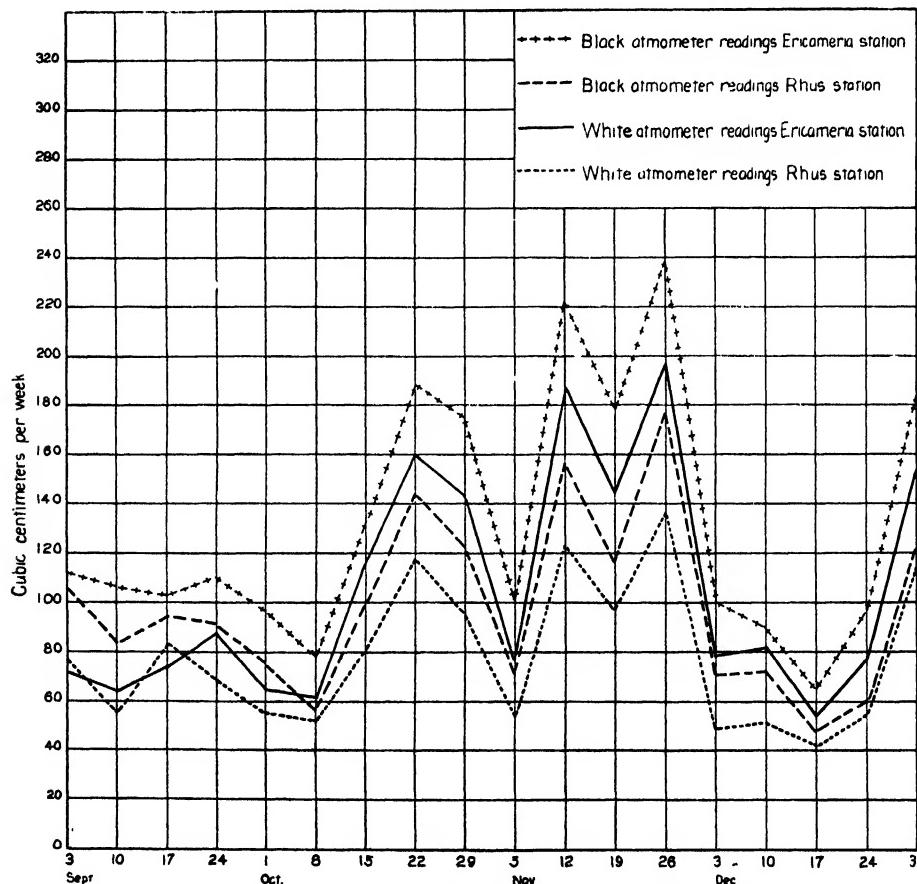
FIG. 5. Evaporation from black and white atmometers at two stations, Ericameria (3), and Rhus (4), El Segundo, Los Angeles County, September, 1932 to January, 1933.

breakers is an additional factor, especially at the Abronia station. Slopes facing south are more xeric than those facing north, this being due, not to the wind which in general is from the west, but to the sun and the resulting higher temperature.

WIND

The prevailing wind at San Diego is from the west, with an average velocity of 5.3 miles per hour for 1930, 6.6 for 1931 and 6.5 for 1932.[7] At Los Angeles the prevailing wind for most of the year is from the southwest, the average velocity being 4.5 miles per hour in 1930, 5.9 in 1931, and 5.8 in 1932.[8] The wind attains a velocity of twenty-eight to thirty miles per hour at times, this being sufficient to blow salt spray inland for a considerable distance. Sandblast, caused by wind-carried sand, carves living twigs (Cowles, 1899) as shown by Rhus in San Diego County. It is a probable cause in the limitation of the height of shrubs, as observed in Rhus on the Silver Strand. Thickets of Rhus in that location were found, too, to be partially dead on the side exposed to strong winds.
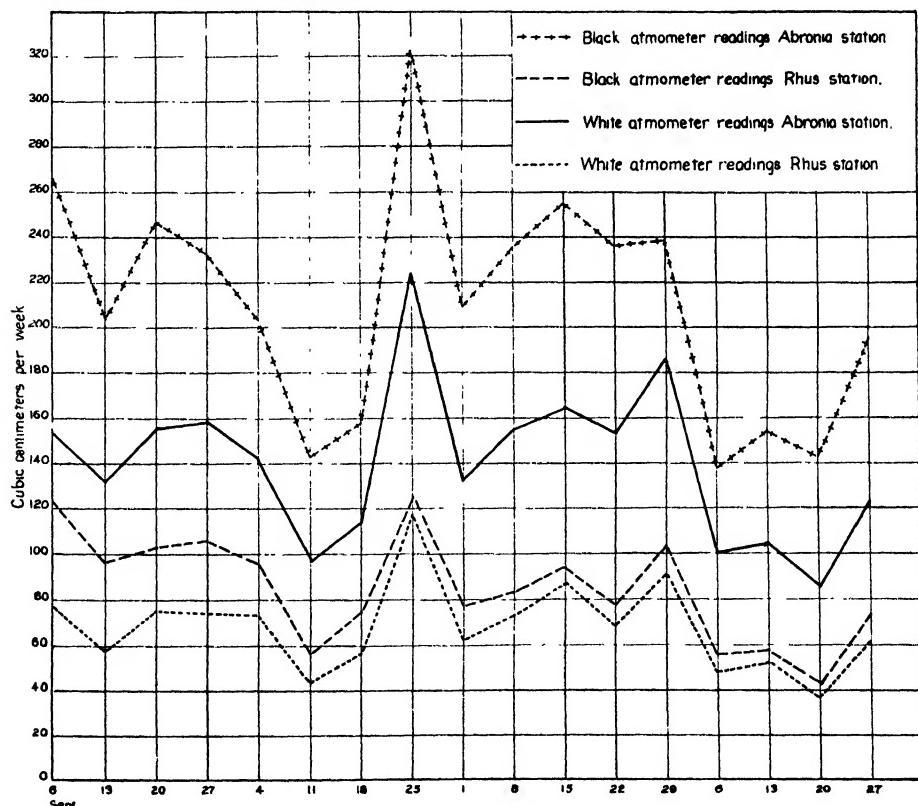
FIG. 6. Evaporation from black and white atmometers at two stations, Abronia (5), and Rhus (6), Silver Strand, San Diego County, September, 1932 to January, 1933.

[7] Weather Bureau, U. S. D. A., San Diego.   [8] Weather Bureau, U. S. D. A., Los Angeles.

PRECIPITATION

Precipitation records[9] for San Diego and Los Angeles show a fairly close correlation. About ninety per cent occurs from the beginning of November to the end of April.

PRECIPITATION IN INCHES

SAN DIEGO

Year	Month	Monthly Maximum	Total for Year
1930	Jan.	3.90	11.73
1931	Feb.	4.11	15.16
1932	Feb.	5.15	11.34

LOS ANGELES

Year	Month	Monthly Maximum	Total for Year
1930	Jan.	5.57	13.02
1931	Dec.	5.95	18.93
1932	Feb.	5.33	10.72

Figs. 3 and 4 give the total monthly precipitation for three years, from January, 1930 to January, 1933. Comparison of temperature graphs with charts of total monthly precipitation at each locality shows that the period of the maximum precipitation does not coincide with that of maximum temperature; rain comes at the season which is most unsuitable for growth, the cold part of the year, and when the temperatures again become favorable for growth there is little or no precipitation.

Precipitation, while of interest for a comparison of various dissimilar dune areas, is approximately the same at the six stations established in the two dune areas investigated as appears to be indicated by the San Diego and Los Angeles records of the Weather Bureau. Therefore precipitation itself probably has but little differentiating effect on the plant life at the several stations.

While much of the rain quickly percolates to the water table and becomes unavailable to plants whose roots are in the upper layers of the sand, these plants may, nevertheless, obtain some moisture from that condensed on the surface of the sand. This condensation is due to rapid lowering of the temperature of the soil near the surface on summer nights.

If the supply of sand and the wind velocity may be considered as constant factors, the duration of the dry periods of the year may be said to govern the magnitude of a dune area. On the southern California littoral sunshine plays a large part in sand drying, sand being transported on all but a very few days of the year. The most favorable seasons for dune formation, however, are summer and autumn, especially that period just preceding the rainy season. In 1930, 1931, and 1932, the wind velocity averaged 4.9 miles per hour during August and September at Los Angeles and 6.2 miles per hour at San Diego. Some further facility is afforded then to sand transportation by wind, because, with the shortage of water, there is almost a cessation of

[9] Weather Bureau, U. S. D. A., Los Angeles and San Diego.

growth of sand-binding species, and this stabilizing element is then temporarily lessened.

HUMIDITY

The manner in which information on relative humidity is recorded at the Federal Weather Bureau stations is such that no satisfactory conclusions could be drawn from that source. The investigation of humidity, therefore, rests upon information obtained by means of a cog psychrometer at two stations established at the sand dunes, Abronia (5) and Rhus (6), on the Silver Strand. Weekly records were secured at approximately the same time of day over a period of four months, from September, 1932 to January, 1933. This interval included dry weather, which was broken in December by the advent of the winter rains. During these four months the percentage of relative humidity did not drop below fifty and on one day attained one hundred per cent. (See Table 3.)

TABLE 3. Relative Humidities at the Abronia and Rhus Stations (Silver Strand) between 3:30 and 4:30 P.M.

1932	Abronia station			Rhus station		
Date	Dry bulb Fahrenheit	Wet bulb	Relative humidity %	Dry bulb Fahrenheit	Wet bulb	Relative humidity %
September 27.......	65	58	66	64	58	70
October 4.......	67	59	62	67	58	58
11.......	63	58	74	66	61	75
18.......	64	57	65	65	58	66
25.......	68	59	58	69	60	59
November 1.......	64	60	79	67	64	85
8.......	69	59	55	68	58	54
15.......	62	59	84	64	59	79
22.......	60	58	89	60	58	89
29.......	62	58	79	61	59	89
December 6.......	60	56	78	59	56	83
13.......	51	51	100	51	51	100
20.......	61	56	73	60	55	73
27.......	63	58	74	62	56	69

SOIL CHARACTER

Soil samples collected at each station at depths of 25, 45, and 75 centimeters, were sent for analysis to the Bureau of Chemistry and Soils, U. S. D. A., Washington, D. C.

The samples, except that taken from the bluff, represent loose, incoherent sands, and range from rather coarse to medium grades. The component of highest percentage is quartz, ranging as high as ninety per cent, with a little feldspar and considerable basaltic material. Minute fragments of shells were found in some of the samples. The coarsest sands were at the Abronia while the finest were at the two Rhus stations. Dune soils are poor in nutrient materials; organic substances which may be left in the soil are rapidly de-

composed, and, owing to the physical structure of sand, rain water carries humus particles deep into the soil. This general type of soil is very permeable to water, since the soil particles possess little cohesion because of the porous structure of sand and its deficiency in colloidal material. There is usually a rapid drying of the surface after rains, the thin dry top layer probably conserving the soil moisture. In light rains, water may be evaporated from the surface before it can be absorbed by the soil.

SOIL MOISTURE

Determinations of water-content were made monthly at the Silver Strand, San Diego County, at the Abronia (5) and Rhus (6) stations from May, 1932 to February, 1933. Samples were taken at 10, 20, 30, 40 and 60 cm. A spade was used and the samples collected in numbered and weighed bottles. Each soil sample was obtained by pushing the mouth of the bottle into freshly exposed sand, and immediately thereafter the bottle was tightly stoppered. The first weighings were made within an hour after securing the soils and were carried out to thousandths of a gram. The sands were then dried in their open containers for forty-eight hours at a temperature ranging from 103 to 107 degrees Centigrade. The percentages of water were computed upon a dry weight basis, using:

$$\frac{\text{wet weight - dry weight}}{\text{dry weight}} \times 100 = \text{percentage of soil moisture.}$$

Table 4 and Table 5 give the percentages from May, 1932 to February, 1933, of the Abronia and the Rhus stations, respectively. This interval includes the critical period of the year, when there is but little moisture in the soil, and the period of rains of early winter.

During the rainy season there is an abundance of soil moisture except at the surface, which dries soon after a rain. During spring and early summer the water content decreases steadily; later in the summer, and until the early winter rains set in, the amount of water available is so slight that it is probable the plants suffer from a water deficit. As Cooper (1922) found in the case of a chaparral area, so also in these dunes in the present investigation a lag in the response of the lower layers of the sand to the first rains was noted, which shows that the advent of precipitation does not close the dry season in such layers of the sand as are occupied by the deep roots of Lupinus and Ericameria. Somewhat, too, as stated by Cooper for chaparral, there are three causes for the depletion of water in the dune soils. These are drainage of gravity water, evaporation from the surface of the sand, and water removal by plants. Shortly after the end of the rains the gravity water is removed from the upper layer of soil, while evaporation from the surface

TABLE 4. Percentage of moisture in soil at Abronia station (5).

Date	Depth cm.	Wet weight gms.	Dry weight gms.	Percentage of moisture
1932 May	10	109.62	109.07	.49
"	20	84.79	84.03	.90
"	40	72.81	71.48	1.80
June	10	105.45	104.90	.51
"	20	104.39	103.79	.57
"	30	85.30	84.19	1.30
"	40	96.94	95.60	1.40
"	60	91.62	90.08	1.70
July	10	83.38	82.97	.49
"	30	103.80	102.60	1.30
"	60	101.70	99.90	1.80
August	10	112.97	112.33	.56
"	20	110.92	110.31	.55
"	30	110.15	108.75	1.30
"	40	104.02	102.40	1.50
"	60	61.39	60.22	1.80
September	10	110.31	109.75	.51
"	20	101.71	101.16	.54
"	30	105.13	104.39	.71
"	40	100.07	98.32	1.70
"	60	104.59	103.18	1.30
October	10	107.19	106.93	.25
"	20	106.20	107.40	.74
"	30	102.94	102.35	.58
"	40	107.44	106.70	.69
"	60	106.99	106.27	.68
November	10	107.54	105.73	1.70
"	20	102.81	100.47	2.33
"	30	98.59	96.01	2.69
"	40	109.21	106.16	2.88
"	60	106.48	105.12	1.39
December	10	105.44	104.84	.57
"	20	101.35	99.52	1.84
"	30	101.71	98.77	2.97
"	40	101.92	99.07	2.88
"	60	101.79	98.59	3.24
1933 January	10	195.02	194.06	.87
"	20	196.60	195.74	.75
"	30	198.41	196.97	1.26
"	40	191.86	191.04	.74
"	60	193.18	191.56	1.48

continues for a longer period. Removal by plants continues during the year, or until such time as all available water has been removed.

SOIL TEMPERATURE

For determinations ordinary Centigrade chemical thermometers and maximum and minimum thermometers were used. When taking soil samples, chemical thermometers were inserted in the freshly exposed sand at different depths at the Abronia (5) and Rhus (6) stations on the Silver Strand. Surface temperatures were also taken in sun and shade, the bulb of the thermometer being thrust into the sand just below the surface. These data were

Table 5. Percentage of moisture in soil at Rhus station (6).

Date	Depth cm.	Wet weight gms.	Dry weight gms.	Percentage of moisture
1932 May	10	106.00	105.39	.58
"	20	100.67	98.06	.26
"	40	101.62	98.78	.28
June	10	99.47	98.83	.65
"	20	100.01	99.24	.77
"	40	92.16	90.42	1.80
"	60	95.33	93.91	2.50
July [10]	..	......	......	....
August	10	103.94	103.43	.49
"	20	107.63	106.98	.60
"	30	102.27	101.60	.65
"	40	83.00	82.02	1.00
"	60	82.60	81.70	1.10
September	10	107.20	106.72	.44
"	20	104.39	103.79	.57
"	30	103.95	103.29	.62
"	40	103.14	102.22	.89
"	60	99.32	98.52	.81
October	10	100.29	98.90	1.40
"	20	97.79	94.10	3.90
"	30	100.26	97.64	2.60
"	40	94.26	92.48	1.10
"	60	97.56	96.81	.78
November	10	97.45	94.92	2.66
"	20	92.43	89.59	3.15
"	30	93.92	90.64	3.67
"	40	84.26	80.35	4.86
"	60	97.55	94.61	3.10
December	10	97.89	95.83	2.15
"	20	100.93	97.76	3.25
"	30	100.00	97.07	3.02
"	40	96.54	93.11	3.69
"	60	98.44	94.96	3.67
1933 January	10	181.59	175.54	6.53
"	20	180.97	178.90	2.13
"	30	179.13	171.54	8.44
"	40	174.88	166.97	9.31
"	60	189.58	185.66	3.81

[10] Data lacking for this month.

obtained from June, 1932 to January, 1933, and in the case of the Rhus station some additional data became available for March, April and May. All these are given in Tables 6 and 7.

Following approximately the methods of Toumey and Stickel, 1925, maximum and minimum thermometers were placed horizontally at a depth of 45 cm. in wooden boxes constructed so as to prevent circulation of air while at the same time permitting ready access to the instruments. This installation was made at five stations, namely, El Segundo, moving dune station (2), Ericameria (3), and Rhus (4), and at the Silver Strand, Abronia station (5) and Rhus (6). Readings were taken weekly from September, 1932 to January, 1933 (Table 8).

TABLE 6. Soil temperatures at Rhus station, Silver Strand.

Depth cm.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
						Degrees Centigrade				
Surface in sun........	....	..	37	35	37	42[11]	36	32	25	cloudy
Surface in shade.....	25	28	30	31	32	30	30	24	22	20
10	22	25	26	32	32	30	27	20	20	18
20	19	20	21	28	29	25.5	25	19	18.5	18
30	18.5	19	20	25	25	25	24	19	18	17
40	....	..	..	24	24	25	23	20	18	17
60	....	..	..	23	24	24	22	20	18	17

TABLE 7. Soil temperatures at Abronia station, Silver Strand.

Depth cm.	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
			Degrees Centigrade				
Surface in sun...........	36	38	43[11]	37	33	23	cloudy
Surface in shade.........	29.5	30	30	29	25	18	18
10	31	31	27	25	19	20	18
20	27	27	26	23.5	18.5	18	17.5
30	26	25	24	22	19	18	17.5
40	24	23	23	22	19	18	17.5
60	22.5	22	22	21	20	19	17.5

[11] Temperatures taken in August in forenoon instead of afternoon.

The maxima at the five stations show considerable uniformity, the moving dunes exhibiting the greatest differences. For the week ending December 3, 1932, the maximum temperature at the moving dune station at El Segundo was seventy-four degrees Fahrenheit, ten degrees higher than at the Abronia and Rhus stations on the Silver Strand and nine degrees higher than the Ericameria and Rhus stations at El Segundo, the smallest differences occurring at the Rhus stations. The minima show more uniformity on the whole, with the exception that during this period of four months, the lowest minimum recorded, for the week ending December 17, 1932 at the El Segundo moving dune station, was eleven degrees less than at the Abronia station, Silver Strand, for the same period. By comparison of maxima and minima at any one station it becomes evident that the temperature range from week to week is small, usually four to eight degrees, running higher at the Abronia station, while at the moving dune station on two occasions the weekly range was fourteen degrees. Throughout these four months in which the lowest temperature, forty-five degrees, was reached but once, in December, there was no time during which low temperature could have affected metabolic processes seriously or prevented root growth.

Soil temperatures at the surface and at about ten centimeters depth are not only higher at times but are also subject to greater fluctuation than those at greater depths. Thus roots which are close to the surface, are subject to

TABLE 8. Weekly maximum and minimum temperatures.

Date	Abronia Silver Strand		Moving dunes El Segundo		Ericameria El Segundo		Rhus Silver Strand		Rhus El Segundo	
	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.
	Degrees Fahrenheit									
September 3......	80	73	82	72	76	70	74	71	74	69
" 10......	79	72	80	72	76	71	74	69	72	69
" 17......	78	70	74	68	74	70	71	69	71	68
" 24......	76	70	75	72	71	70	70	69	72	69
October 1......	76	68	77	67	72	66	70	68	75	67
" 8......	74	67	75	67	74	66	71	66	73	66
" 15......	73	65	74	64	73	65	67	65	69	65
" 22......	68	59	75	61	71	63	69	60	68	60
" 29......	70	60	74	67	67	63	67	64	65	61
November 5......	68	60	74	65	67	61	66	62	64	60
" 12......	71	59	74	66	66	62	66	62	69	60
" 19......	68	59	73	65	65	61	66	63	63	59
" 26......	66	60	73	62	67	60	65	62	65	58
December 3......	64	57	74	63	65	58	64	59	65	56
" 10......	68	56	69	62	63	56	62	53	65	51
" 17......	68	56	59	45	57	48	58	52	61	47
" 24......	58	52	61	52	57	48	62	52	59	47
" 31......	58	52	62	49	55	50	59	52	56	51

the influence of an environment which is quite different from that affecting roots growing at deeper soil levels.

BIOTIC FACTORS

Biotic factors do not exert a marked influence in the sand dune habitat. This, in itself, constitutes an important feature, being responsible for much of the distinctive character of the vegetation. No earthworms, which play so beneficial a rôle in certain other soils, are to be found here. Where the vegetative cover has become established small accumulations of humus may occur, and during the rainy season mushrooms are found growing here and there. A rather important influence is that of the fires which occasionally run through the later stages of the plant succession.

AUTECOLOGY OF ELEVEN SAND DUNE SPECIES

THE SPECIES

Floristically considered, the coastal sand dunes of southern California contain a large number of annual plants, over 50 species being represented in San Diego County. The study of these, however, has been limited in the present work to their identification, since they are of little importance in succession, tiding over the long unfavorable period in the form of seeds. All of

the species investigated are perennials, existing under adverse conditions for the greater portion of the year over a number of years, and showing more or less modification for their environment.

Out of the large number of perennials inhabiting these coastal dunes, certain species were selected which are preëminent because of their positions in the succession, their distribution, and their adaptation to the environment, as attested by their abundance and successful maintenance.

METHOD OF INVESTIGATION

Field studies were made of the coastal dunes from Florence, Oregon, to Ensenada, Baja California. In these the locations of each of the chosen species on the strand, the moving dunes, and the stabilized areas, were noted. Each species was investigated as to its range, its actions as pioneer or invader, and its ability to endure covering by sand. At least ten examples of each species were examined, the size, gross morphology, type of branching, rate of growth, time of flowering, depth of roots, and types of roots being noted.

Measurements of the entire plant were made in the field. For the root system the surface sand about the plant was removed. Pieces of lumber, 4 by $\frac{7}{8}$ inches, by 8 feet, were driven into the sand and then nailed together to prevent a cave-in. The distance from the plant at which this structure should be constructed was carefully estimated to prevent the planks from interfering with a root or being forced upon it, thereby breaking or injuring it. Photographs of the plant were taken during the process of excavation.

Measurements of the root systems were made as follows: after some of the surface sand had been removed, enabling a rough location of the more important roots, the general extension and the directions of the parts of the root system were carefully noted. The whole area estimated to be occupied by roots was then crossed by tapes firmly attached to stakes, marking off one-foot squares. The actual locations of the roots were obtained by careful digging with trowel and hands. For recording the horizontal locations a paper divided into one-inch squares was used. Each square inch representing one square foot of ground was subdivided into 100 smaller squares. For recording vertical distribution the horizontal record was made use of in connection with a vertical projection of the root system, depths being obtained by measurement. For representing the aerial portions of the plant, measurements were taken before excavation of the root system was begun. The vertical drawing includes shoot as well as root system, the horizontal drawing the lay-out of the root system only. In the vertical drawings, the root systems which come in a nearly vertical plane are shown, those at right angles being indicated by a dot when they diverged from the vertical. The horizontal plan represents the entire root-system as seen from above. If, for any reason, roots were not followed to their termination, the diagram indicates this by a

broken line. Weaver's (1927) methods were followed as closely as possible. Later, when the plant was excavated, in order to verify the measurements, the entire root system and the aerial portions as well were remeasured.

For minute characteristics, material collected in both areas was used. In order to obtain a representative size, mature leaves were measured over a period of a year in order to include both the dry and rainy seasons. From 50 to 200 specimens of each species were employed for this purpose.

Leaves, herbaceous and ligneous stems, and roots were sectioned in the investigation of the minute anatomy. The leaves and stems were gathered from the upper portions of vigorous plants, that were fully exposed to the prevailing environmental conditions. Slides were made of fresh material as well as of material embedded in paraffin and celloidin. For killing plant material formal-acetic alcohol was employed. Various stains were tried—light green, gentian violet, fuschin, safranin, orange G, and Bismarck brown. Microtome sections from ten to twenty microns in thickness were cut, the thickness depending upon the character of the material.

Tests for mucilage, resin, oil, cutin, and certain other substances, were made on fresh material.

When the count of the stomata was difficult to obtain, the epidermis was covered with a commercial collodion preparation. After drying, this collodion film was peeled off, and from it stomatal counts were made.

ABRONIA MARITIMA NUTT.

HABITAT

Abronia maritima grows upon the first or foredunes, the embryonic dunes which rise from the uppermost part of the strand. It may, however, extend its prostrate branches upon the very surface of the strand, where possibly winter's highest storm waves may reach them. At that season of the year the waves frequently lash at these dunes, exposing the roots of Abronia and often undermining small dunes. *Abronia maritima* is associated with few plants on the strand. Occasionally it may be found growing with Franseria and Atriplex.

This Abronia, because of its activities, is the principal pioneer, beginning its development in fresh-blown sand. The species, however, may be found also in locations a considerable distance from the ocean where the older, longer stabilized vegetation has not succeeded in holding the sand and movement has begun. For this reason there does not seem to be any correlation between *Abronia maritima* and proximity to salt water or salt spray. Fungi are frequently found growing in small mounds of Abronia where humus has collected.

AERIAL PARTS

The stems of *Abronia maritima* are prostrate, forming a mat that in some cases may reach a size of fifty by twenty-five feet. When sand collects around the plant an upright position is maintained by the support thereby afforded. When sand ceases to collect about the plant the branches, being too heavy to stand upright, fall to the surface of the sand with just the tips abruptly extending upward, making the plant at most about eight inches in height. From the center a large number of branches extend in all directions, forming a mat of vegetation which aids in the fixing of the sand and in the formation of a dune.

The stems and leaves are stout and fleshy, the usually unequal leaves of a pair being vertical in position, broadly ovate to oblong, round at the base, obtuse, irregularly slightly undulate, and with stout petioles. The average[12] length of leaf (blade with petiole) is 4.0 cm.; without the petiole, 3.0 cm. The width is 2.0 cm.; thickness, 2.9 mm. Fleshy leaves of plants on the strand at the sand dunes near Guadalupe averaged 5.5 mm. in thickness.

Buds form at all seasons, but are most abundantly produced in spring.

SUBTERRANEAN PARTS

The root system consists of a tap root with a few secondaries, the roots being strong and tough, but not extensive (Pl. 1). The system as a whole, has very few absorptive roots as compared with those of some of the other species considered. The maximum depth attained, unless covered by drifting sand, is about two feet. Two or three feet of spread from the tap-root may be expected, but aerial stems, buried in the soil, may aid in spreading the plant farther. Although the tap-root may be thick at its juncture with the stem, it tapers rapidly and comes to an abrupt end. In some of the excavations on the strand, the tips of the roots were found to be dead several inches above the level of the salt water. Sand collected from just below the ends of such roots showed a slight saline reaction.

ANATOMY OF THE STEM

The major tissue of the stem is water accumulative, mechanical tissue being small in extent. In the epidermal layer, averaging 0.025 mm. in width, with its many well-developed, multicellular, glandular trichomes, are occasional, slightly sunken stomata. The epidermis is covered by cuticle,[13] 0.002 mm. thick. Solereder (1908) states that the deposition of crystalline granules, consisting of calcium oxalate, occurs in the cell-walls of the epidermis of stem and leaf in Abronia.

Below the epidermis there is a layer of chlorenchyma as wide as the epidermis. Inside of the chlorenchyma, water accumulative tissue occurs,

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[12] Throughout this paper, unless otherwise stated, an average for each species was obtained from at least fifty specimens, but for the most part one hundred were used.
[13] The use of the term "cuticle" in this paper is that given by Eames and MacDaniels, 1925

composing from one to two-thirds of the diameter of the stem. This tissue is composed of cells three to six times the thickness of the epidermal cells. Bundles of raphides consisting of long acicular crystals of calcium oxalate are present here (Pl. 2).

Concerning the stems of the Nyctagineae, Solereder (1908) says:

The anomaly consists in the appearance, in the pericycle, of successive rings or strips of cambium, which produce secondary collateral vascular bundles, and conjunctive tissue on their inner side. The prosenchymatous conjunctive tissue bears simple pits like the wood-prosenchyma of the vascular bundles, from which it is difficult to distinguish, and is sometimes traversed by typical medullary rays.

Within the secondary vascular bundles are the primary, with pith parenchyma occupying the center of the stem, the pith being well developed.

ANATOMY OF THE LEAF

The most noticeable feature of the leaf is the large amount of water accumulative tissue, extending throughout the leaf between the epidermal surfaces. The epidermis averages 0.04 mm. in width, being about equally thick on both sides. Leaves from a prostrate stem usually assume a vertical position which affords equal lighting on the two sides. Both epidermal surfaces bear about the same number of closely placed, uniseriate, multicellular, glandular trichomes, in length about five times the diameter of the epidermis. These trichomes have spherical heads, which are larger than the cells of the stalk. The petioles are also covered with glandular trichomes.

The stomata, on both surfaces, are somewhat sunken and are surrounded by glandular trichomes. The stomatal count[14] averages twenty-one per square millimeter on the adaxial surface and twenty on the abaxial. The cuticle is about 0.005 mm. thick on either surface.

The leaf is of the diplophyll type bearing chlorenchymatous cells, many of them enlarged and containing water, and frequently about six times the diameter of the epidermis in length. Chloroplasts are very numerous, scattered throughout the cells, and average 2.80 to 3.15 microns in diameter. They appear to be smaller toward the center of the leaf, and are found even in the water tissue around the veins. The intercellular space system is scanty. The cells of the water tissue were turgid at all times when examined, except that during the rainy season they seemed to be slightly less turgid than during the dry season. Bundles of raphides of calcium oxalate occur in the water accumulative tissue.

Measurements of the thickness varied considerably, depending upon the location in which the specimens were gathered. The average thickness of 2.9 mm. is exclusive of the trichomes, these increasing the thickness by 0.4 to 0.6 mm. Leaves of plants near the ocean were thicker than those collected inland.

[14] Pieces of epidermis were stripped from the periphery and from near the midrib because of variation in the number per unit of area. In all cases at least ten specimens were used.

ANATOMY OF THE ROOT

The roots of *Abronia maritima* do not show any special adaptations. The older roots and those near the surface or exposed to the air, are covered with a layer of bark. In younger roots a layer of cork surrounds the cortex, which is composed of large parenchyma cells. The anomalous structure of the roots corresponds with that of the stems, in that there is a concentric arrangement of secondary vascular bundles and of parenchyma formed within the pericycle. The xylem of the vascular bundles has large tracheae. In the pith parenchyma is a ring of these bundles occupying the center of the root.

SUMMARY

While *Abronia maritima* does not have an extensive root system, the character of some of its aerial parts tends to cut down the water loss and to hold water for use during unfavorable periods. Since the species is a prostrate plant, the desiccating effect of winds is largely avoided. The approximately vertical position of the leaves permits the rays of the sun to strike them at an angle, whereby transpiration is probably reduced and less reflected light from the sand received.

Some modifications are: diplophyll type of leaf, with most of the leaf converted into water accumulative tissue; presence of trichomes on both surfaces of the blades, and on the petioles and stems; cuticle; few stomata per square millimeter; stomata slightly sunken: death of some of the leaves during drought, some of them remaining on the plant and affording some protection from wind and sun.

Since this species is usually on or near the strand, its root system could not extend to a great depth without reaching salt water. To aid the organism in tiding over the rainless season, the plant depends not only upon water absorbed by the roots but also upon water in the form of dew or fog absorbed by the leaves.

Growth is apparently not influenced by the salt spray deposited upon plants growing near the strand, since such specimens are as healthy as those in open areas removed from the strand.

CONVOLVULUS SOLDANELLA L.

HABITAT

Convolvulus is found on sandy sea beaches, growing on the strand and in open places in the dunes. It is not usually associated with other plants, but is found in flat areas between hummocks overgrown by *Abronia maritima* and Franseria, and has not been found in habitats other than sand dunes.

AERIAL PARTS

This species has a prostrate growth habit, with its subterranean portion more extensive than observations of the aerial parts would indicate. The rhizomes grow about 4 to 6 inches below the ground surface, one specimen, only partly excavated, extending 55 feet and bearing numerous branches. From the alternate nodes of a rhizome there arise short upright stems with small clusters of from four to six foliage leaves (Pl. 3). In spring the stem may rise to the surface, form a small arch and return to its level in the soil, or it may continue its growth for several feet along the surface.

The thick, succulent leaves are reniform and of a deep green color, the adaxial surface glabrous and shining. The average length of a leaf (blade and petiole) is about 5.0 cm., the length and the width of the blade 1.8 cm. and 4.0 cm., respectively, and the thickness 0.50 mm. The petioles are stout, white to red in color, with considerable variation in length. The branch tips bear three to six turgid green leaves, while those farther from the tips soon become yellow and flaccid.

SUBTERRANEAN PARTS

The rhizomes of Convolvulus are succulent, pink to tan, varying from 25 to 50 feet in length. Short roots about 6 inches in length, develop from the underground stem at the nodes, the absorptive system being thus very meager.

ANATOMY OF THE STEM

The most noticeable internal feature of the stem is the large amount of succulent tissue. The entire stem is composed of this with the exception of the vascular tissue and epidermis. A transverse section of the aerial stem presents a somewhat irregular outline. The epidermis, 0.025 mm. thick, has but few stomata and is covered with cuticle of about 0.002 mm. thickness. On the inner side of the epidermis the cells of water accumulative tissue gradually increase in size toward the center. Anthocyanin is present within the cells just below the epidermis, but no chloroplasts were found. The vascular system is of the dictyostele type composed of bicollateral bundles with but little development of tracheae and tracheids. Of the stems that were examined, the pith occupies less than one-third of the diameter.

The underground stem is about two to three times the diameter of the aerial stem and is of similar structure. No stomata or chloroplasts were found in the rhizomes.

Non-anastomosing laticiferous vessels are found in the cortical and in the pith parenchyma of both the aerial stem and the rhizome, being especially abundant in the latter (Pl. 4).

ANATOMY OF THE LEAF

The leaf epidermis, about 0.03 mm. thick, with walls slightly thicker on the outside, is covered with a fairly heavy layer of cuticle, averaging 0.004 mm. on the adaxial surface and 0.003 mm. on the abaxial. The stomata, which appear in both surfaces, are but slightly sunken in the epidermis, and are accompanied by two subsidiary cells. There are about 155 stomata per square millimeter on the adaxial surface; 150 on the abaxial. The stomata average 0.035 mm. long and 0.040 mm. in width, including the subsidiary cells.

Below the adaxial surface are from three to six rows of palisade cells. Somewhat more than one-half of the mesophyll in the abaxial portion of the leaf is composed of compact spongy chlorenchyma. Small acicular crystals are found in the mesophyll, usually grouped into bundles of raphides. The latex occurs in large laticiferous ducts located on the adaxial side of the larger veins. There is little intercellular space except near the stomata on the abaxial surface, the palisade layers on the adaxial surface being particularly compact. The succulent appearance of the leaf is due to the large amount of water in the chlorenchymatous tissues.

ANATOMY OF THE ROOT

In a transverse section of younger roots small patches of collenchyma are seen. In older roots the development of phellogen results in a narrow layer of cork, within which the cortical parenchyma, composed of rather large cells, occupies about three-fourths of the diameter of the root, with a circle of multicellular laticiferous tubes at regular intervals. Starch grains were found to be abundant in the cells of the cortical parenchyma. The endodermis is well defined; the xylem of the stele consists of a few tracheae surrounded by wood fibers.

SUMMARY

The low habit of growth of Convolvulus off-sets the desiccating influences of the sand dune habitat. Its rhizomes are very succulent, due to the presence of a large proportion of water accumulative cells and latex vessels. The root system is meager as compared with that of the other ten species investigated. The epidermis which is covered with cuticle has numerous stomata in both surfaces of the leaves; stomata occur only sparingly on the aerial stems. The cells of all tissues are very closely placed, leaving but a small proportion of intercellular space.

ATRIPLEX LEUCOPHYLLA DIETR.

HABITAT

This perennial Atriplex generally forms small hummocks in the open areas of the strand. It grows rather close to the ocean, often associated with *Abronia maritima* and sometimes with Franseria.

AERIAL PARTS

The plant is reclining or, when sand accumulates around it, maintains itself in an upright position for not more than six inches above the surface. In all specimens excavated the stem branching began at 6 to 8 inches below the surface; with progressive burial the stems grow upward. The spread is about 2 to 3 feet from the crown of the tap root (Pl. 5).

Branches are numerous, alternate in arrangement, very short and stout, and somewhat woody at the base.

The pale green leaves are densely scurfy, thick, orbicular to elliptic, entire, sessile, three-nerved, acute, averaging 1.0 cm. in length, 7.0 mm. in width and 3.2 mm. thick at the mid-rib.

SUBTERRANEAN PARTS

The root system is fairly extensive as compared with the shoot system. In all the plants excavated it was found to consist of a tap-root extending 2 to 4 feet below the surface, its length depending upon the amount of burial by sand. Secondary roots coming from the tap-root extend at different levels as far out as the aerial parts extend.

ANATOMY OF THE STEM

The epidermis, bearing stomata, is densely scurfy with overlapping trichomes. These are vesicular hairs, composed of one-celled scales and one to two-celled stalks. Scales are of two sizes, the larger about eight times as long as the width of the epidermis. The walls of the epidermal cells are of equal thickness on all sides, the cuticle being about 0.002 mm. thick. At the inner side of the epidermis there are two to three rows of collenchyma cells. The young stem develops a few groups of chlorophyll-bearing parenchyma cells slightly larger than those of the epidermis. The cells of the cortical parenchyma, in size about three times that of the epidermal cells, act as water accumulative tissue and contain large druses of calcium oxalate. The conducting system is a large polyarch dictyostele with collateral vascular bundles. The center of the stele is occupied by an extensive pith, whose cells contain druses. The tissues of the stem are compact, with little intercellular space, except near the occasional stomatal structures. Anthocyanin is present in the epidermal layer and in a few cell layers beneath it. As growth proceeds, the anomalous structure of the stem becomes evident in the development of secondary vascular bundles (Solereder, 1908).

ANATOMY OF THE LEAF

The leaf is thickly covered on both surfaces with trichomes of vesicular hairs which are of two sizes, the larger two to three-celled, the smaller unicellular. The length of the larger is greater than the diameter of the leaf.

The epidermis, about 0.015 mm. thick, consists of a single layer of cells, whose walls are of equal thickness. Both the epidermal surfaces are covered with a thin layer of cuticle, about 0.0025 mm. thick on the upper surface and 0.0016 mm. on the lower. Slightly sunken stomata are present in both layers. The stomatal count for the adaxial surface was one hundred per square millimeter; for the abaxial one hundred and ten. The average length of a stoma is 0.023 mm. and its width 0.015 mm. Below the epidermis is a layer of water accumulative tissue in which are special cells bearing large druses of calcium oxalate. This leaf differs from all others of those investigated in that the palisade tissue does not appear directly below the epidermis but is located under one or more layers of water accumulative tissue. The veins are surrounded by a zone of chlorenchyma, the midrib, however, possesses only two lateral patches.

The tissues are compact, with few intercellular spaces, except in the immediate vicinity of the stomata.

Solereder (1908) referring to the Chenopodiaceae states that

the most noteworthy features in the structure of the leaf are the absence of a definite type of stoma, and of typical spongy tissue, which has not been observed in any species. In spite of the xerophilous character of many species the cuticle rarely attains a considerable thickness, nor have mucilaginous epidermal cells been observed.

The leaf in cross section measures on the average 0.75 mm. including the trichomes, and 0.25 mm. without them; at the midrib it is about 0.91 mm. thick (Pl. 6).

ANATOMY OF THE ROOT

There is a thin layer of cork on the mature root beneath which there is cortical parenchyma composed of large, thin-walled cells. After secondary thickening has developed, the cortical parenchyma is present as a rather narrow zone. The anomalous structure of the root is seen in the formation of pericyclic rings or strips of cambium, which form concentric zones of vascular tissue and thin-walled parenchyma cells (Solereder, 1908).

SUMMARY

While Atriplex has frequent stomata per unit of area on both surfaces of the leaf and on the stem, excessive transpiration is probably checked by the scurfy surface and by over-lapping trichomes, which provide a dead air space above the epidermis. Transpiration is probably further retarded by the slightly sunken stomata, the closely placed cells, and the presence of cuticle. Water is retained in peripherally placed water accumulative tissue. The extensive xylem of the root system may serve to supply this plant advantageously with water when the soil moisture is ample. Light does not reach the chloroplasts readily, due to the trichomes and to the embedding of the chlo-

renchymatous tissue. This species appears to be able to withstand sand cover-
ing as it is usually found growing in a partly buried condition. It appears to
thrive in unstable soil exposed to severe wind, where evaporation rates are
high, heat intense, and direct and reflected light strong.

MESEMBRYANTHEMUM AEQUILATERALE HAW.

HABITAT

The character of the soil does not appear to be of great importance for
this species, since it is found on sand and on sandy and clayey loams of
coastal dunes and bluffs, making its best growth, however, on the sand dunes.
It occurs in the foredunes behind the strand, and in rear portions of the dunes,
either alone or associated with any of the species of the more stabilized areas.
Since it is a sand-binder and dune-former, making its appearance usually
after such a true pioneer as *Abronia maritima* and others of its sort, it may be
classed as a secondary pioneer. Mesembryanthemum is often employed under
cultivation as a sand-binder.

AERIAL PARTS

The species is a prostrate perennial herb, forming extensive mats, often
fifteen to twenty feet in diameter. Much of the older portions of the plant
dies during late summer and autumn, before the succeeding rainy season be-
gins. Water is conserved by the younger branches until the rainy season
commences, and the plant is thus carried over the critical period.

Young stems are fleshy, non-terete, and almost as great in diameter as the
leaves. In age the stems shrink radially and become hard and brittle.

Succulence is due mainly to the fleshy leaves which are three-sided, oppo-
site in pairs, without stipules, and mostly nearly vertical in position. Their
nearly flat sides are smooth and somewhat less broad than the thickness of
the leaf. A leaf averages about 5.0 cm. in length, 1.2 cm. in width on the
wider face of the inequilateral triangle, and about 0.9 cm. wide on the other
two faces.

SUBTERRANEAN PARTS

The fibrous root system is meager as compared with the size of the plant,
completely lacking the extensive branching observed in many of the dune
species. The roots are all superficial, and consequently efficient in absorbing
the moisture from light rains and from condensation of water vapor of fogs
and dew upon the soil, but the roots are unable, from their superficial char-
acter, to obtain water which is located much below the surface. Since the
plant develops roots at the nodes as the stems grow extensively over the sur-
face of the ground, sand-binding is a prominent feature. Many new roots
develop after the beginning of the winter rains, but none becomes extensive
either in length or diameter (Pl. 7).

ANATOMY OF THE STEM

The young stems are very fleshy, and their epidermis bears stomata, but lacks trichomes; it is covered with a layer of cuticle, 0.005 mm. in thickness. On the inner side of the small epidermal cells, as seen in transverse section, are two to three rows of small round chlorenchymatous cells. The rest of the cortex is composed of cells which vary in size from about that of the epidermal cells to about six times their diameter. In these cortical cells, with their large percentage of water, giving the stem its succulence, are found occasional chloroplasts and many bundles of raphides; small vascular bundles are interspersed. A conspicuous endodermis surrounds the stele. In the center of the stem is the vascular tissue which appears somewhat oblong in cross-section. The cells of both the tracheids and tracheae are very small as compared with those in the succulent tissue, while the tracheae are small in number as well. The stem, in which no vascular rays are present, is anomalous in structure due to the peculiar arrangement of the concentric vascular areas (Solereder, 1908). In the center is the pith in which are occasionally deposited bundles of raphides. The younger stems of this species contrast strongly with those of the other plants investigated as regards their extreme succulence and small amount of mechanical tissue. The older stems, with only their conductive tissue in use, are brown and shriveled.

ANATOMY OF THE LEAF

The triangular leaf has its epidermis,[15] which is 0.02 mm. thick, covered on all three sides of the leaf with a heavy layer of cuticle, about 0.004 mm. in thickness. Stomata on all three surfaces have an outer stomatal chamber formed by an overhang of the two subsidiary cells. The guard cells, small in size, are sunken to the inner side of the subsidiary cells; below them is located the inner stomatal chamber. There are on an average about 90 stomata per square millimeter on the adaxial surface of the leaf, and about 86 per square millimeter on the two abaxial surfaces. The length of the stomata averages about 0.04 mm. and the width, 0.03 mm., including the subsidiary cells.

For a comparison of stomatal counts, a Mesembryanthemum plant of the same species, probably an escape from cultivation, growing in a shaded location in a vacant lot in Los Angeles, was examined. Its stomata numbered 280 per square millimeter on the adaxial surface and 268 on the two abaxial surfaces, the size of the stoma also differing. On the adaxial surface of the leaf the length of the stoma averaged 0.01 mm. while on the abaxial surfaces, it was slightly more than 0.015 mm. in length and 0.005 mm. in width.

In the sand dune habitat the palisade tissue, directly under the epidermis on all three sides of the leaf, is composed of two to three rows of long and

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[15] According to H. Solereder (1908), "in Mesembryanthemum it [calcium oxalate] also occurs in a deposition in the cell wall in the form of small crystalline granules, found principally in the outer wall of the epidermal cells of the leaf."

narrow cells with chloroplasts lining their walls. This tissue comprises but little of the total volume of the leaf. Sclereids are found at intervals in the palisade, and these mechanical cells extend from the epidermis to the succulent tissue. They are Y-shaped and closely placed in the palisade, which is very compact except at the stomatal openings. On the inner side of the palisade tissue the entire leaf, except for the vascular bundles, is composed of large-celled succulent tissue, many of these cells being ten times as long as those of the epidermis. Bundles of raphides, consisting of needle-shaped crystals of calcium oxalate, occur frequently in these. Among the palisade cells are long and wider cells containing mucilage, while in the succulent tissue there are very large, rounded and sometimes elongated, mucilage cells (Pl. 8).

The vascular system, as seen in cross-section, consists of small cells and is comprised of a principal bundle in the center of the leaf with smaller bundles in the succulent tissue; a parenchymatous sheath of small cells surrounds the principal bundle. A patch of sclerenchyma is located on the outside of the phloem.

ANATOMY OF THE ROOT

The root contains underneath its epidermis large cells of cortical parenchyma, these acting possibly as water accumulative tissue, to judge from the succulence of the young root. In the cortical parenchyma bundles of raphides are occasionally present. The anomalous structure of the stem is repeated in the older root by its concentric rings of xylem and parenchyma (Solereder, 1908).

SUMMARY

Since the root system is a shallow one, the plant must depend upon succulence to maintain it through the dry summer months. It is a common occurrence for the older parts to die, and this to so great an extent that only half a dozen of the green triangular leaves may remain at the end of each stem at the close of summer. This procedure is of great assistance in maintaining the plant during the critical period. Leaves were examined at all seasons of the year, and it was observed that during the dry period the leaves which remained green were as turgid as leaves on similar plants in the rainy period.

The position of the leaf is vertical, affording thus reduced exposure to direct rays of the sun. Being three-sided, the leaf has a small surface exposure in proportion to its volume. Protection from desiccating winds is afforded by the low position. Both young stems and leaves, consisting mainly of water accumulative tissue, are extremely succulent, there being but a small quantity of conductive and practically no mechanical tissue. The epidermis is heavily cutinized and the stomata are well protected within the epidermal layer both by their position and by the over-hang of their subsidiary cells.

FRANSERIA BIPINNATIFIDA NUTT.

HABITAT

This perennial is a sand binder and stabilizer rather than a dune former, although at times sand collects around the plants, forming small hummocks, the species being capable of withstanding slow burial. The highest rates of evaporation were obtained at the station where this species grew, indicating it existed under the most severe environmental conditions in the dunes as far as evaporation was concerned.

AERIAL PARTS

Franseria is a perennial whose ascending axis soon comes to be more or less reclining, the stems attaining a length of 2 to 3 feet. Branching is alternate or opposite, the internodes on reclining branches being three to four times as long as those on vertical branches. The alternate or opposite leaves, are twice to thrice pinnately dissected into irregular oblong lobes, and are canescent or almost silky with slightly recurved edges. The length of the leaf (blade and petiole) averages 5.0 cm., the length of the blade being about 3.7 cm. and its width 3.5 cm., while the thickness of the midrib, including the trichomes, is 0.90 mm., and without them, 0.60 mm.

SUBTERRANEAN PARTS

The root system is not extensive, reaching in most plants excavated to a depth of about three feet. Secondary roots are produced from the lower portion of the fleshy tap root.

ANATOMY OF THE STEM

The epidermal layer of the young stem, somewhat irregular in transverse outline, is covered with cuticle 0.002 mm. thick. Multicellular, unbranched, overlapping, pointed trichomes are frequent, often as long as twelve times the width of the epidermal layer. On the inner side of the epidermis of the younger stem the isodiametric cells of the cortical parenchyma contain chloroplasts; older stems have five to six rows of collenchyma inside the epidermal layer. In younger stems the cells of the cortical parenchyma become larger toward the center and, at intervals in this tissue, forming an irregular ring immediately outside of the vascular bundles and generally alternating with them, occur patches of specialized parenchyma cells with anthocyanin, giving the appearance of a duct, while in older stems no such disposition of anthocyanin occurs. In addition to these anthocyanin patches, there are located in the chlorenchyma groups of about two to four parenchyma cells containing anthocyanin in their cell sap.

The conducting system is a dictyostele with a group of sclerenchyma fibers on the outside of the phloem part of the bundle. The pith of the young stem,

distinctly of the herbaceous type, occupies over three-fifths of the diameter in
transverse section, with druses commonly present in its cells. Later the cell
walls of the pith thicken and become lignified, but the amount of pith does
not decrease greatly with age (Pl. 10).

ANATOMY OF THE LEAF

The adaxial surface of this diplophyll leaf is covered with a layer of
cuticle 0.005 mm. thick, and the abaxial with a layer 0.003 mm. thick. The
epidermal cells, 0.02 mm. in thickness, are heavy walled and of about equal
size on both surfaces, each of which bears narrow, pointed, multicellular,
unbranched trichomes. The tip cells of the trichomes are abruptly pointed or
long pointed. Stomata, slightly sunken, are about 153 per square millimeter
on the adaxial surface, and 150 on the abaxial, with a length of about 0.025
mm. and a width of 0.020 mm. Several rows of palisade cells occur under
both the adaxial and abaxial surfaces, while in the center of the leaf are larger
cells of spongy parenchyma containing here and there a few chloroplasts.
These tissues, especially the large cells in the center of the leaf, contain an
abundance of water, making the leaf succulent. Small druses are found
throughout the mesophyll. In the region of the midrib the mesophyll consists
of more or less rounded parenchyma cells, while in the rest of the leaf the
mesophyll is of a more compact parenchyma containing a rather large propor-
tion of elongated cells. In the vicinity of the midrib, on the adaxial surface,
palisade chlorenchyma is lacking for a short distance, the space being occupied
by parenchyma tissue, while on the abaxial surface there are two layers of
palisade cells. Leaves vary in thickness in different locations in the dunes.
Those near the strand were usually found to be two to three times thicker
than those farther inland. The spongy parenchyma frequently becomes water
accumulative in the thicker leaves.

ANATOMY OF THE ROOT

On roots of approximately two mm. diameter the cork layer is three to
four cells thick. The cortical parenchyma, composed of numerous thin-walled
cells, contains a circle of schizogenous ducts. A few other similar ducts are
scattered irregularly within this circle and occasional ducts are located outside
of it. No differentiated endodermal layer was found. The conducting sys-
tem is a dictyostele with the phloem and cambium well marked; the xylem
contains some large tracheae and rather broad vascular rays; there is no pith.

SUMMARY

Franseria, of the eleven species considered, grows under the severest dune
conditions, under the highest evaporation rates, where there is little soil stabil-
ity, with great exposure to wind and high temperature as well as to intense
light. Under these xeric conditions the species shows the following modifi-

cations: low growth form; leaves much dissected and slightly recurved at the margin, presenting less superficial area; both sides of the leaves silvery, due to the presence of numerous overlapping trichomes which almost completely cover the epidermal surface. The stem is likewise covered with trichomes. The stomata, few per unit of surface, are slightly embedded in the epidermis. The root and stem contain some water accumulative tissue.

OENOTHERA CHEIRANTHIFOLIA HORNEM. VAR. SUFFRUTICOSA WATS.

HABITAT

This sand dune evening primrose is found on the upper portions of the strand beyond the storm-swept areas, and in stabilized locations farther from the ocean; it frequently grows alone in open sand areas, and also associated with *Abronia umbellata, Erysimum capitatum* (Dougl.) Greene, *Lupinus chamissonis* and *Eriogonum parvifolium.* Since it appears in bare areas and aids in stabilization, it may be classified as a pioneer, though it is of secondary importance in this respect, being less valuable than *Abronia maritima* and *Franseria bipinnatifida* in forming small dunes and in holding the sand.

AERIAL PARTS

Oenothera has a spread of about 2 feet, its branches radiating from a central rosette which crowns the taproot. The stems are mostly decumbent to prostrate, but when growing close to shrubs a plant may attain a height of one foot. It is somewhat woody near the crown.

The alternate leaves are thick and covered on both surfaces with short, dense, appressed trichomes, resulting in a silvery-canescent appearance. The shape of the obtuse leaf varies from obovate to oblong-lanceolate, with an entire or sinuate-toothed margin. On the basis of leaves collected at different seasons, the length of the leaf (blade and petiole) averages 2.0 cm., length of blade 1.8 cm. and the width 0.9 cm. The leaves which appear in spring are about twice as long as and considerably more flat than those produced during late summer and autumn. Upper leaves are sessile while the lower are usually petioled.

SUBTERRANEAN PARTS

The root system is a meager one. It consists of a tap root, slightly fleshy near the surface of the ground, extending to a depth of about three feet in an average specimen; it bears a few lateral roots (Pl. 11).

ANATOMY OF THE STEM

The epidermis, which contains anthocyanin, bears unicellular, unbranched trichomes of two sizes. The larger are in length about thirty times, while the

smaller are about ten times the diameter of the epidermal cells. The epidermis is covered with a layer of cuticle 0.002 mm. in thickness.

Below the epidermis are a few rows of isodiametric collenchyma cells. To the inner side of these is a region of slightly larger cells of cortical parenchyma, some of which contain bundles of raphides. A few rows of small chlorenchymatous cells enclose the stele. In stems of 2.0 mm. diameter, the stele shows a continuous cylinder of xylem, consisting mainly of tracheids with some small tracheae, without indication of separate vascular bundles. The vascular rays are very narrow and probably always uniseriate. The cells of the pith parenchyma are somewhat larger than those of the cortical parenchyma, and later become lignified; bundles of raphides occur in some. Many of the stems were found to be hollow.

ANATOMY OF THE LEAF

Large, appressed, unicellular, unbranched trichomes cover both epidermal surfaces. They point toward the leaf tip, covering the blade. The small, rather thin-walled epidermal cells are similar on both surfaces, averaging 0.018 mm. in thickness. Cuticle, about 0.003 mm. thick on the abaxial surface is but slightly thicker on the adaxial. Stomata, lying even with the surface, are found on both epidermal layers. The guard cells average 0.025 mm. in length and 0.017 mm. in width.

The leaf is of the diphotophyll type with its mesophyll chlorenchymatous throughout. Below the adaxial epidermis are two layers of closely placed palisade cells. Below the palisade layers about one-half of the mesophyll is occupied by spongy chlorenchyma consisting of small, rounded, loosely disposed cells. The veinlets, surrounded by parenchymatous bundle sheaths, are numerous. Small bundles of raphides occur in the cells of the mesophyll while very large bundles appear to have extended themselves through several cells and intercellular spaces.

The leaf in cross-section averages 0.64 mm., including the trichomes, and without them 0.36 mm., while at the midrib the leaf measures 0.70 mm. with the trichomes, and without them 0.42 mm.

In plants of the more xeric conditions stomata average 170 to the square millimeter on the adaxial surface and 285 on the abaxial. On ten plants with larger leaves in a more mesic habitat, the stomata averaged 250 to the square millimeter on the adaxial and 354 on the abaxial surface.

In some instances, as in more mesic dune conditions, the diphotophyll type of leaf with two layers of palisade on the abaxial surface is displaced by the diplophyll with one layer of palisade under the abaxial surface.

ANATOMY OF THE ROOT

The root develops several external layers of suberized cells. Its cortical parenchyma is probably for water accumulation, since the root becomes

slightly fleshy below the root crown. The well developed stele contains a small proportion of phloem, back of which lies the broad xylem zone containing numerous tracheae (Pl. 12).

SUMMARY

This evening primrose grows in the more xeric habitats of the sand dunes. Its structural modifications are shown chiefly in its growth-form and somewhat in its internal anatomy. It is low growing and well-rooted. The leaves, slightly fleshy, are silvery-gray in color, being covered with a thick layer of overlapping trichomes. Many of the leaves are shed during the dry season. The palisade layers are compact and aid in reducing transpiration.

LUPINUS CHAMISSONIS ESCH.

HABITAT

Lupinus is not found on the strand or in the foredunes, and while it grows on the most exposed areas in wind swept blow-outs and often on the very crest of the dunes, withstanding there the severest winds, it becomes established best in locations where the wind is not active in moving the sand and in areas where establishment of other species has already taken place. From atmometer readings at stations near Lupinus, evaporation rates were found to be less than in communities of *Abronia maritima* on the strand. The Rhus community, however, has a lower and less variable evaporation rate. Lupinus is found alone in wind swept areas or associated with Ericameria, *Abronia umbellata* and Eriogonum in partly stabilized sections.

AERIAL PARTS

This erect woody evergreen shrub, with numerous stout branches which are leafy throughout, attains a height of 4 to 5 feet and a horizontal extent of about four feet. The alternate leaves are palmately compound, consisting of four to nine leaflets which are somewhat folded, forming a V. The leaflets are cuneate-obovate, obtuse to acute, and silky on both sides. The petioles are dilated at the base and bear at the upper end of the dilation two stipule-like lanceolate appendages at either side of the petiole. The length of the leaf averages 2.5 cm., the leaflet blade on the average being 1.6 cm. in length with a width of 4.2 mm. The autumn aspect of the species shows the leaves more V-shaped in cross-section and more rolled than in other seasons.

SUBTERRANEAN PARTS

The root system is very extensive; one plant 2 feet in height had a root spread of 13 feet at a depth of 11 feet, this representing an average condition. The customary tubercles of leguminous plants occur on the roots (Pl. 13).

Anatomy of the Stem

The epidermis of the young stem, covered with cuticle 0.004 mm. thick, bears closely placed, exceedingly long, unbranched, multicellular trichomes. On stems, whose diameters are slightly over 1.0 mm., the trichomes are as long as the stem is wide, being exceeded in length in the other species studied only by occasional trichomes on the stem of Oenothera. The trichomes consist of an enlarged epidermal cell, a short stalk cell, and a long filiform terminal cell. To the inner side of the epidermis occurs one, or sometimes two, rows of chlorenchyma and below this tissue are several rows of large cells of cortical parenchyma. From the sclerenchyma areas at the outer ends of the vascular bundles, as seen in cross-section, there runs a more or less continuous ring of sclerenchyma. Pith, consisting of large cells, composes about one-half of the cross-section of the young stem, while the older stem becomes woody, with a large cylinder of xylem in which there is an irregular development of tracheae in a cylinder composed principally of tracheids (Pl. 14).

Anatomy of the Leaf

The epidermal layer of a leaflet is about 0.015 mm. thick on each surface, covered by cuticle about 0.003 mm. in thickness varying to about 0.002 mm. on the abaxial side. Both surfaces of the blade, and the petiole with its extensions, bear a large number of long, narrow, unbranched, multicellular trichomes, in total length about seven times the width of the epidermis. They consist of an enlarged epidermal cell, a short stalk cell, and a long terminal cell.

The stomata projecting slightly beyond the epidermal surface, average about 150 to a square millimeter on each side of the leaf and measure about 0.030 mm. in length and 0.025 mm. in width. The entire leaf inside of the epidermis is composed of rather closely placed palisade tissue, except at the center, where there is some spongy chlorenchyma in which are veins surrounded by a parenchymatous sheath. The conducting system is composed of one large vascular bundle at the midrib, which is one-fourth the thickness of the leaflet at that point, and of a number of smaller bundles distributed through the center of the leaf. The leaf measures about 0.35 mm. in thickness exclusive of the trichomes, and with the trichomes 1.10 mm.

Anatomy of the Root

The younger root is covered with a small amount of cork and contains a wide layer of cortical parenchyma; in the older root the latter becomes much reduced with the increasing width of the xylem. The phloem is rather small in size while the xylem contains a liberal number of rather large tracheae, and has conspicuous one to three-seriate vascular rays extending well out into the cortex.

SUMMARY

Lupinus is found in stabilized areas or sometimes occupies the same position in the dunes as does Franseria in the more exposed positions where the greatest evaporation and the severest conditions of instability prevail. The root system is very widespread and deep, the most extensive of those investigated. Instead of broad leaves it has V-shaped leaflets, as seen in cross section, offering less surface exposure to the sun, and becoming thereby much less rapidly heated. The leaves, like those of Franseria, are covered with overlapping trichomes, resulting in a silvery appearance and providing a still air space between the trichomes and the epidermis. Due to the abundance throughout of palisade tissue, the leaf is compact with very little intercellular space, and loss of water is consequently reduced. The young stems bear long filiform trichomes, giving them a silvery appearance similar to that of the leaves.

ERIOGONUM PARVIFOLIUM SM.

HABITAT

This woody perennial shrub, sometimes attaining four feet in height, occurs not only on the sand dunes, but also on the hillsides near the coast. In the dunes it is found on stabilized sand or on hummocks in unstabilized areas, usually where Franseria has already become established. Its other common associates are the species of Rhus, Lupinus, Ericameria and *Abronia umbellata*, though with respect to these other dune plants, Eriogonum may be considered as of secondary importance.

AERIAL PARTS

The shoot system has a spread of about 3 feet, and is made up of stems that are white-tomentose when young, becoming reddish with age, the alternate branches bearing densely fascicled leaves.

The leaves are oblong-lanceolate to ovate, obtuse, truncate to subcordate at the base, the margin undulate and irregularly revolute. The peculiarities of this margin, a conspicuous feature of the leaf, are most noticeable in autumn. Young leaves are covered with a mat of intertwined hairs on both surfaces; at maturity they are very dark green and shiny above, and covered with a dense white felt beneath. The length of the leaf (blade and petiole) is about 2.7 cm.; the blade, 1.2 cm.; its width about 1.2 cm.

The young petiole is short and broad, clothed with trichomes on the abaxial surface and less abundantly so on the adaxial; in maturity the petiole becomes less flat, longer and less hairy.

SUBTERRANEAN PARTS

In the plants examined, the tap root extended to a depth of approximately four feet and the branch roots spread out three times as far as the parts above ground, with considerable irregularity in the root distribution (Pl. 15).

ANATOMY OF THE STEM

The younger stems have epidermal trichomes of two kinds: non-glandular trichomes that are narrow, filiform, unicellular, and about ten to twelve times as long as the width of the epidermis, which is about 0.013 mm. in thickness. The multicellular glandular trichomes about three times the diameter of the filiform trichomes consist of four or five cells and are in length somewhat less than four times the thickness of the epidermis. The bicellular head, formed by a vertical wall, is larger than the cells of the stalk. Under the epidermis there are a few rows of cortical chlorenchyma, while to the inside of this tissue is cortical parenchyma containing a number of large druses of calcium oxalate. Surrounding older stems there is a band of sclerenchyma about four cells in thickness. The stem is a dictyostele. The xylem has small tracheae; vascular rays are about three cells in breadth. Occupying the center, and composing about one-half of the younger stem in transverse section, is the pith in which are present a few druses; the older stems become hard and frequently hollow.

ANATOMY OF THE LEAF

The principal feature of the leaf is the wide layer of palisade tissue. Below the upper epidermis the dense palisade tissue is composed usually of three rows of large sized cells, extending through three-fourths of the thickness of the leaf. Beneath this is a narrow band of veins, with small parenchymatous cells in which are found druses. Between this zone and the lower epidermis are two rows of short but closely packed palisade cells. Large water accumulative cells are found at the midrib, many filled with large druses of calcium oxalate. The thickness of the blade, about midway between the midrib and the margin, is almost 0.30 mm. exclusive of the trichomes; including the trichomes it is about 0.65 mm. Fleshy leaves, found on plants near the ocean, measured midway between midrib and margin 1.10 mm., exclusive of the trichomes. The thickness at the midrib is about 0.70 mm., exclusive of the trichomes.

The adaxial epidermis, covered with cuticle which is about 0.002 mm. thick, is about 0.013 mm. in thickness, with heavy cellulose walls. The abaxial epidermis, less than 0.01 mm. thick, and covered with cuticle 0.001 mm. thick, is composed of cells less than half the size of those on the adaxial surface. Stomata are present only in the abaxial epidermal layer; they are slightly sunken and number about 282 to the square millimeter. The epidermal

trichomes on the petiole and on the abaxial surface of the blade are of two kinds: plain trichomes, which are very long, filiform, and unicellular, and short glandular, multicellular trichomes. The filiform trichomes appear to come from narrower cells than those of the regular epidermis, the length of these trichomes being as great as the diameter of the blade. The glandular trichomes have a two to three-celled stalk with a head made bicellular by a vertical wall (Pl. 16).

ANATOMY OF THE ROOT

The root of this species differs but little from that of most woody plants. No succulent tissue, so frequent in the roots of some of the other ten species, was observed. To the inside of the cork are a number of rows of cortical parenchyma, and irregular groups of sclerenchymatous cells occur in the cortical parenchyma and in the phloem. The xylem, in a root 3.0 mm. in diameter, occupied two-thirds of its cross section, with vascular rays one to two cells in width, the conspicuous feature of the xylem being the abundant and frequently large tracheae.

SUMMARY

The leaves of Eriogonum are very closely placed on the stem and have revolute edges, affording thus a reduced transpiring surface without a change in volume. The thick cuticle on the adaxial surface gives the leaf a glossy appearance. which probably aids in the reflection of light. Since glossy leaves become more slowly heated than others, evaporation is thereby probably reduced. Nearly all of the leaf, except for a narrow band of veins, consists of closely placed palisade with little intercellular space. The abaxial surface alone has stomata, which are sunken in the epidermis. Crystals are present in the leaf and the stem. Two kinds of trichomes, both on the stem and the leaf, are so abundant as to present the appearance of a dense felt.

ABRONIA UMBELLATA LAM.

HABITAT

This species does not compete with *Abronia maritima* on the strand, the foredunes, nor the more unstable areas, but it may grow near the strand in slightly protected locations. *Abronia maritima* and *A. umbellata* frequently have been found growing side by side, but this proximity is due to the fact that *A. maritima* established itself after a stabilized area had become unstable again, the *A. umbellata* being a remnant from a more mesic and stable community.

The latter is associated with such genera as Ericameria, Eriogonum and Lupinus in the stabilized areas, and on mounds of Franseria in more open spaces.

AERIAL PARTS

This sand-verbena is prostrate, with very slender stems about 3 to 5 feet in length, widely branching from the crown of a fleshy root. On several occasions it was observed that Abronia, growing in rather dense vegetation, had changed from its prostrate form to a climbing form in scrambling over a shrub. Its vegetative growth, with its slender stems and slight leaf development, is inadequate to cope with sand movement as compared with the sturdy growth of *Abronia maritima*. The height of the aerial portions, which is generally about 4 to 5 cm., depends on the total length of the leaf when the stems are prostrate, as is usually the case.

The stem is viscid-puberulent, generally reddish, with long internodes and opposite branching.

The leaves of a pair are unequal. They are flat, thick, obtuse, broadly obovate to oblong, with slightly sinuate margins. The position of the leaves is more or less vertical from the prostrate stem. The mature leaf (including blade and petiole) is about 4.0 cm. in length. The length of the blade is 2.3 cm., the width 2.3 cm., and the thickness 1.1 mm.

SUBTERRANEAN PARTS

The root system is more extensive than in *Abronia maritima,* and there is not so much burial of stems by sand in *A. umbellata*. When, however, the wind causes an accumulation about established plants they become partially covered. The spreading of the plant from its center is brought about by means of aerial and not underground portions. The tap-root, fleshy just below the surface of the soil, may extend to a depth of 4 to 5 feet. Lateral roots spread one to three feet from the tap-root (Pl. 17).

ANATOMY OF THE STEM

The stem is composed largely of water accumulative tissue. Its epidermis, bearing infrequent stomata, is 0.01 mm. thick, covered with cuticle 0.002 mm. thick, and with a scattering of multicellular glandular trichomes. Anthocyanin may be found in the epidermal layer.

The cells of the cortical parenchyma, some of which contain chloroplasts, are about two times the diameter of the epidermal cells. Bundles of raphides of calcium oxalate are present in some. On the upper side of the stem the cells contain more chloroplasts than do those on the lower side, due to greater exposure to light.

The endodermis is clearly differentiated. Solereder (1908) states that a ring of cambium inside of the pericycle produces on its inner side secondary collateral vascular bundles and parenchyma tissue. The parenchymatous cells are pitted, giving them the appearance of woody tissue. Pith, with some cells containing bundles of raphides, occupies the center of the stem in which

is disposed a ring of separate vascular bundles. Little mechanical tissue is present.

ANATOMY OF THE LEAF

The diplophyll leaf is made up chiefly of palisade tissue. Its epidermis is covered with a layer of cuticle, 0.003 mm. thick, and bears a few multicellular glandular trichomes, which have spherical heads larger than the cells of the stalk. The epidermis, with anthocyanin in most of its cells, is 0.025 mm. thick, being practically the same on both sides of the leaf. The epidermal cells are round to rectangular, except that those serving as bases for the hairs are larger and somewhat triangular in the leaf cross section.

The remainder of the leaf is composed of chlorenchyma, in which there are about six rows of palisade. Regularity of palisade tissue is not as prominent a feature in Abronia as in the leaves of the other species investigated. Numerous chloroplasts, some bundles of raphides, and considerable water are found throughout the palisade. Within the leaf blade are a few cuboid cells of spongy chlorenchyma, and small vascular bundles, around each of which is a parenchymatous bundle sheath (Pl. 18).

About 50 slightly sunken stomata per square millimeter occur on the adaxial surface and about 60 per square millimeter on the abaxial. Their guard cells are 0.040 mm. long and 0.025 mm. wide. The epidermal cells of the petiole of the leaf and the edges of its blade contain conspicuously more anthocyanin than do the epidermal cells of the general leaf surfaces.

ANATOMY OF THE ROOT

The fleshy tap-root bears a corky layer which is comparatively heavy without being bark-like in character, at least within the limit of present observations. The cortical parenchyma is composed of large thin-walled cells about six cells thick in roots 2.0 mm. in diameter. The remainder of the root structure is the same as in *A. maritima*, with pith parenchyma and a concentric arrangement of secondary vascular bundles. Bundles of raphides are present. There is but little phloem and the xylem contains few tracheae.

SUMMARY

· The species conserves water by a low habit of growth, vertically placed leaves, small number of stomata per unit area, presence of cuticle, compact tissue of palisade character, and a small amount of intercellular space. The plant is adjusted to the sand dune environment somewhat differently than its close relative, *A. maritima*, in possessing less succulence and a deeper root system. *A. umbellata* conserves water by the death of the older leaves during the dry part of the year, while in *A. maritima* only a few leaves die then. *A. umbellata* produces seeds abundantly, propagating by this means rather than vegetatively, as does *A. maritima*. *Abronia umbellata* is not as succulent, has fewer trichomes and more stomata per unit area than *A. maritima*.

ERICAMERIA ERICOIDES (LESS.) JEPSON

HABITAT

Ericameria is found for the most part in locations where there are sand dunes somewhat removed from direct wind action, and the species is one that can endure some covering by sand. It is associated with those plants which come into the partly stabilized dune areas, such as Lupinus, Eriogonum and Rhus.   Occasionally, *Lotus scoparius* (Nutt.) Ottley, *Abronia umbellata* Lam., *Galium angustifolium* Nutt., and *Erysimum capitatum* (Dougl.) Greene are associated with it.

AERIAL PARTS

This evergreen shrub attains an average height of about 3 feet. Its main stems are mostly upright while the peripheral branches often become decumbent and yet have numerous erect branches, making the plant about 4 feet wide. Ericameria has a xeric appearance, with a heather-like herbage of alternate linear-terete leaves. The somewhat pubescent leaves and stems are resinous. The leaves, occurring in fascicles, are somewhat vertically placed, the lower leaf being longer than the others, averaging a little less than one centimeter. Measurements of the lower leaf made after the rainy season averaged 1.4 cm. in length, while the other leaves, placed between this and the stem, averaged less than 1.0 cm. The thickness from the dorsal to the ventral surface of a leaf averaged 0.56 mm. and its width 0.70 mm.

SUBTERRANEAN PARTS

The root system is extensive, the tap and secondary roots extending downward eight or more feet into the soil in an average adult specimen, while the horizontal spread of the roots is about five times as great as the spread of the aerial parts. The roots grow uniformly in all directions at the different depths of their distribution (Pl. 19).

ANATOMY OF THE STEM

The stem is very tough and woody, even when young, and while young its epidermis bears long filiform trichomes of about three cells, consisting of one or two small cells near the surface and an extremely long terminal cell. Cuticle, about 0.002 mm. thick, covers the surface. There are about 40 stomata per square millimeter. Beneath the guard cells and the adjacent protruding epidermal cells, large stomatal chambers occur. In the older stem there is a superficial development of cork, and in the younger stem, below the epidermis, a narrow band of cortical parenchyma in which are bundles of acicular crystals and resin canals apparently of schizogenetic origin. A group of sclerenchyma cells is located outside of the phloem part of each vascular bundle. The stem is of the dictyostele type with collateral bundles, the xylem,

with a few tracheids and numerous small tracheae, is well developed. The frequent vascular rays are conspicuous, being three to four cells in width. The central pith, with a few cells containing bundles of acicular crystals, is small and definite, occupying about one-fifth of the diameter of the stem, as seen in transverse section in the specimens examined (Pl. 20).

ANATOMY OF THE LEAF

The minute needle-like leaves, are terete, with a groove on the adaxial side. The epidermis, having numerous filiform trichomes when young and entirely smooth when old, is 0.030 mm. thick, and is covered with a layer of cuticle 0.005 mm. thick. The guard cells are about even with the epidermis. Stomata, arranged in rows, are present on all sides of the leaf, and possess large stomatal chambers. The stomata average approximately sixty per square millimeter, and are about 0.010 mm. long and 0.006 mm. wide. Nearly three-fourths of the leaf tissue is composed of dense palisade in which are acicular crystals[16] of calcium oxalate.

The center of the leaf is occupied by spongy chlorenchyma which also partly surrounds the three resin canals; close to these, the three vascular bundles composing the vascular system are located.

Leaf size varied in different locations in the dunes, being larger than the average on plants located near the ocean, and owing this increased size mainly to a larger proportion of palisade tissue.

ANATOMY OF THE ROOT

Young roots develop a cork layer inside of which are a few rows of small cells of cortical parenchyma, whereas older roots are covered with bark. The root is of a woody type, the xylem, with conspicuous vascular rays and a row of resin-canals, occupying more than one-half of the diameter. There is no pith.

SUMMARY

Ericameria, although found in less xeric habitats than *Abronia maritima* and Franseria, does not occupy the most mesic position in the sand dunes. It has been pointed out elsewhere that when evaporation rates increased at all the stations, these rates were greater at the Ericameria station than at the Rhus station. When the evaporation rates decreased at all other stations, they were also less in the Ericameria, but were usually lower there than at the Rhus station. In other words, there is greater fluctuation at the Ericameria than at the Rhus station. Ericameria is usually found in the stabilized dune areas where there is little movement of the sand, and where the vegetation grows in rather open stands, spaced so as to insure an adequate water supply. The shape of its microphyll leaf gives small surface exposure

[16] According to Solereder (1908), "True raphides are wanting, but occasionally the bundles of acicular crystals come to resemble bundles of raphides."

in proportion to the leaf volume. A heavy cuticle covers the fascicled leaves, while long trichomes cover the younger stems.

RHUS INTEGRIFOLIA B. & W.

HABITAT

This evergreen shrub grows not only in sand dunes but also on clay bluffs along the coast and for some distance inland. In the dunes it is located on stabilized areas, growing best where there is little direct wind. The species is propagated mainly by vegetative means, forming extensive thickets frequently 30 to 40 feet in diameter, with some approximately 100 feet. On older plants the lower branches become procumbent and often take root where they come in contact with the soil.

AERIAL PARTS

The shrub grows to an average height of 5 feet, and in sheltered places may become taller. Plants on the summit of a dune frequently are scarcely 6 inches high while on the leeward side they may attain a height of 6 or more feet. Where the wind commonly has a rather high velocity, the shrub acquires a flat top, with the tips of the twigs dead; this is probably due to the drying effect of wind on the terminal buds. Communities of the plants spread out on the lee slopes of dunes at right angles to the general direction of the wind, seldom becoming circular in outline.

The alternate twigs are stout and stiff. Often in exposed locations dead twigs are found on the windward side of a shrub. At the Silver Strand two lichens, a variety of *Ramalina ceruchis* (Ach.) De Not. and *Dendrographia minor* (Tuck.) Darb., grow on such dead branches.

The leaves are mostly vertically placed, leathery, alternate, elliptic and obtuse. The margin is entire or with a few sharp teeth, which appear to develop on plants of the more xeric locations, though this characteristic is not constant. The leaves (blades and petioles) average 4.5 cm. in length, the blade 4.3 cm. in length, its width 3.1 cm. They are very shiny, doubtless thereby reflecting much light. The color of the adaxial surface is dark-green, while that of the abaxial is much paler. The veins are conspicuous (Pl. 21).

Vegetative reproduction appears to be more frequent and effective than reproduction by seeds. Birds have been noted carrying seeds, but no seedlings and few young plants were observed.

SUBTERRANEAN PARTS

The root system, consisting of a tap-root and an abundance of long secondaries, is extensive, especially when the plant occurs in large thickets. Some of the secondaries extend 10 feet beyond the periphery of the aerial

portion of the shrub. Many of the heavy laterals become exposed through the action of high winds. Adventitious roots occur on procumbent, partly buried branches. Shapiro and de Forest (1932) found that the species is a highly conservative user of soil water.

ANATOMY OF THE STEM

The younger stems are covered with cuticle 0.003 mm. in thickness and bear numerous, unicellular, rather thick-walled, unbranched trichomes which, when fully grown, are in length from five to ten times the diameter of the epidermal cells; the stomata are slightly depressed. At the inner side of the epidermis are several rows of rather thin-walled collenchyma, anthocyanin being present in about six rows but principally in the one adjacent to the epidermis. The remainder of the cortex is occupied by rather small, thin-walled parenchyma cells in which are occasional druses of calcium oxalate (Pl. 22).

A single, large resin canal, partly surrounded by a zone of sclerenchyma, is located in the outermost part of each vascular bundle, in which neither phloem nor xylem is well developed. Tannin was found in the stem. The biseriate or triseriate rays are narrow, and the pith is composed of comparatively small parenchyma cells, some of which contain druses. The most striking features of the stem are the smallness of its cells, the small amount of conducting tissue, and the absence of water accumulative tissue.

ANATOMY OF THE LEAF

The leaf is covered on both surfaces with a thick layer of cuticle, especially on the adaxial side, where it is 0.007 mm. thick, while on the abaxial it measures but 0.004 mm. The adaxial epidermis is 0.037 mm. in width, the abaxial 0.030 mm. The cells are oblong and wider at the surface adjacent to the mesophyll. The stomata, which occur only on the abaxial surface, average 255 to the square millimeter, with guard cells 0.030 mm. long and 0.025 mm. wide. The epidermal cells abutting upon the guard cells are somewhat modified. The epidermis of the abaxial surface bears infrequent, unicellular, unbranched, slightly pointed trichomes, in length about five times the width of the epidermis.

This diplophyll leaf has two layers of well developed, closely placed palisade, below which may be a poorly developed third layer. The first two layers occupy less than one-half of the mesophyll. The rest of the mesophyll consists of irregularly shaped cells, some being somewhat palisade-like in character. Druses of calcium oxalate are present in the mesophyll.

With the vascular bundle of the midrib is associated a large resin-canal, surrounded on the lower portion by several rows of sclerenchyma which extend around the xylem and are continued beyond it to the adaxial epidermis

as a strengthening bar. Veinlets also have resin-canals and sclerenchyma associated with them. Anthocyanin is present in several rows of collenchyma of the petiole, in cells inside of the abaxial epidermis at the midrib, and in groups of cells in the margin of the blade. The margins of the leaf are strengthened by sclerenchyma.

ANATOMY OF THE ROOT

From a phellogen originating in the outer third of the cortex a good development of suberized tissue arises. Within the cortical parenchyma a number of large schizogenous resin passages occur. The phloem is poorly developed. In the xylem, scattered among the tracheids, are well developed and numerous large tracheae; the small vascular rays are mostly uniseriate.

SUMMARY

Rhus integrifolia, the least xeric species of those considered, is more distinctively a member of the chaparral component of the broad-sclerophyll communities of southern California than of the sand dune vegetation. The leaves mostly maintain acute angles with the stem, thus somewhat reducing exposure to light. Both surfaces are well protected by cuticle, which, in addition to the thick outer epidermal wall, renders the leaf stiff. The leaf tissues are compact, especially the palisade below the adaxial surface. The stem and the root are compact in structure, owing chiefly to the smallness of most of the cells. It is probable that the sclerenchyma arranged in a half-column around the vascular bundles aids in maintaining rigidity when there is a deficiency in the water supply. A branch cut and left lying on the sand in the month of June seemed, after a week of exposure, to be as fresh as branches on the shrub.

Rhus integrifolia appears to represent something of a transition between the customary species of a dune complex and those of the chaparral. The stations where Rhus occurs show the greatest stability of the sand and the lowest rates of evaporation as compared with all other stations.

SUMMARY OF AUTECOLOGICAL DATA

INTRODUCTION

The sand dune species of southern California may be divided into two groups: (1) annuals, biennials, or root perennials whose aerial parts appear after the winter rains—growing, blossoming and fruiting, then withering when the dry season approaches; and (2) woody, suffrutescent and succulent perennials which maintain aerial parts throughout the year, even in the most unfavorable period.

Extended consideration will not be given to the first group, since, because of their growth habits, they escape the severe conditions of the habitat during

the unfavorable portion of the year and, consequently, do not exhibit structures suited to such a period, as do the plants of the second group.

GROWTH HABITS

The growth forms in the southern California dunes differ in certain respects from those in some other dune areas. Cowles (1899) has shown that trees, such as the basswood-maple series in the Michigan dunes, form a part of the development. In the Philippines, Kienholz (1926) refers to trees on the upper beach in his study of the beach vegetation, and Cooper (1922) has shown the part trees play in the succession in coastal dunes at Monterey. No trees are present, however, on the southern California coastal dunes. The shrubs for the most part are low and in wind-swept places present a "krummholz" appearance. Portions of some plants exposed to the windward west side of slopes are often much stunted or dead. Where the sand action is pronounced, woody stems sometimes exhibit sand blasting of the bark, and, indeed, some similar effect appears to show occasionally on the leaves themselves. Suffrutescence, though not so markedly developed in the sand dunes as elsewhere, is a characteristic of most of the southern California cismontane vegetation. Oenothera, for example, shows definite suffrutescence. Of the eleven sand dune species investigated the shrubs are low, often decumbent, sometimes spreading and forming thickets over large areas, as in the case of Rhus. The succulent perennials are evergreen and mostly prostrate.

Certain stages in dune development support certain growth forms. There are no shrubs near the strand or in the fore-dunes. These small dunes are held entirely by evergreen perennials, principally *Abronia maritima,* and, to some extent, by the Franseria and the Atriplex. These species are the principal pioneers, especially *Abronia maritima* and Franseria, and are exposed to the most xeric conditions. Couch (1914) in making quadrat studies at Manhattan Beach, Los Angeles County, California, in 1913, found Franseria as a pioneer, followed by *Abronia umbellata* in protected areas. Over flat areas between the hummocks of sand Convolvulus spreads by means of its rhizome habit, acting as a pioneer and stabilizer.

In the moving dune areas Franseria and Lupinus are present. Few annuals are found there, probably owing to the unstable substratum. Active wind movement, soil instability, intense heat and light, and high evaporation rates contribute to the xeric conditions. After pioneers, such as Abronia or Franseria, are more or less established, other species appear as invaders. *Abronia umbellata,* Oenothera, and Eriogonum are chief among these. Such invasion occurs on hummocks in the moving dunes.

Mesembryanthemum plays diverse rôles. Sometimes it is a pioneer just back of the strand, sometimes it is an invader of practically stabilized areas, and sometimes it covers large areas on the leeward slopes of the more or less stabilized dunes.

Still farther removed from the ocean, where wind action is decreased, reflected and diffused light lessened, and the soil relatively stable, shrubs occur in open stands, growing to a height of 4 or 5 feet. Couch (1914) at Manhattan Beach, Los Angeles County, in 1913, found *Abronia umbellata* dominant in one quadrat, with Eriogonum and Lupinus apparently almost codominant in another, while in a third, *Adenostoma fasciculatum* H. & A., was dominant. He states that this last appeared "suddenly," being peculiar to the summit and leeward slopes, but absent from the windward slopes. In the present investigation no succession was encountered in any of the dune areas of southern California in which Adenostoma represented the climax, nor was the species found in any stage leading thereto, although reported by Whitfield (1932) as occurring in Santa Barbara County. Specimens were collected, however, north of southern California in the sand dunes at Seaside, Monterey County, and in areas farther north.

The principal shrub species of the general sand dune complex in southern California are Lupinus and Ericameria, with large, spreading thickets of Rhus in the most mesic habitats.

Along the southern California coast, at several points, true halophytes, such as species of Salicornia, are floristic components of the vegetation of small areas. This does not indicate that the dunes are halic, as explained by Kearney (1904). In the sand these plants showed poor development and were not successful in withstanding covering. They appeared to be relics of an earlier habitat condition. In a saline area on the bay side of the Silver Strand they had become established; then followed an unusual amount of sand movement in which they became partially covered. These plants are now yellow in color and in a dying condition.

SHOOT SYSTEMS (LEAF AND BRANCH)

Stems are of two characters, one with enough stiffening material to stand erect, as in the shrubs Rhus and Ericameria, and the other with little mechanical tissue, as in the case of the Abronias and Convolvulus. Stems of Convolvulus, *Abronia maritima*, *A. umbellata*, and young stems of Mesembryanthemum are very succulent. Variation in surface texture occurs from smooth and shiny in young stems of Mesembryanthemum; silvery-canescent, as in young stems of Lupinus, to cork and bark development in the shrubs, such as Rhus and Ericameria. Growth in length is not rapid in the shrubs, short internodes being characteristic.

Leaves for the most part are small as in Eriogonum and Ericameria; Franseria has lobed leaves; the leaves of Mesembryanthemum are equilateral, while Lupinus has its leaflet blade partly folded. Some leaves have revolute edges, as Eriogonum. Mesembryanthemum, with its thick equilateral leaves, shows the highest degree of succulence; *Abronia maritima* is invariably suc-

culent, though the character of its flat leaves renders this feature much less pronounced than in the former species. *Abronia umbellata* and Franseria are not so succulent, but when growing in areas near the ocean, as at the Silver Strand, they develop this quality to some degree. Convolvulus varies considerably, depending upon the quantity of water accumulative tissue.

WATER CONTENT OF SPECIES

A comparison of the percentages of water in the shoot and the root systems of the representative species was made in August, 1932. Three plants of each species were excavated, the shoot system severed from the roots, each being weighed in the field immediately. Shoots and roots were placed in separate labeled containers and sun-dried for a week. Then they were placed in an oven at 100 to 105°C. until a constant weight was reached. The percentages of water were computed upon a dry weight basis, using:

$$\frac{\text{wet weight - dry weight}}{\text{dry weight}} \times 100 = \text{percentage of water in plant.}$$

Referring to Fig. 7, Convolvulus, Mesembryanthemum, the Abronias, Franseria, and Oenothera had the highest percentages of water in their shoot systems. Their root systems also ran with high percentages, with the exception of Mesembryanthemum. These species are rather shallow rooted, growing in the more exposed situations in the dune habitat. Ericameria and Eriogonum had the lowest percentages of water in their shoot systems and almost as low percentages in their root systems. These species are more deeply rooted, reaching to layers of sand which remain moist for longer periods after rains.

ABSORPTION OF WATER BY AERIAL PARTS

Absorption of water by the shoot system has been demonstrated by a number of investigators. Marloth (1908-10) and Schönland (1908-10) working in South Africa on the same plants, *Mesembryanthemum barbatum* L.., *Crassula cymosa* L. and *Anacampseros filmentosa* Sims., arrived at opposite conclusions in regard to leaf absorption. Demaree (1931) demonstrated absorption in *Taxodium distichum* (L.) Richard, *Sequoia sempervirens* (Lam.) Endl., *Cynara cardunculus* Linn., and in species of Ailanthus, Vitis, Aesculus, Eucalyptus, Quercus and Salicornia. Dandeno (1901) states,

Special parts of leaves of certain plants seem to be adapted to the purpose of absorption as shown by the surface of the epidermal cells over the veins, at the base of the trichomes, and in other regions. Trichomes in some cases are particularly susceptible to the action of water and of solutions applied to them. Striations and hairs or trichomes aid in spreading liquids over the regions which seem to be adapted to absorption; and trichomes prevent a rapid evaporation of the liquid so spread, by retaining air. Absorption of water may take place also through the surface of the petiole.
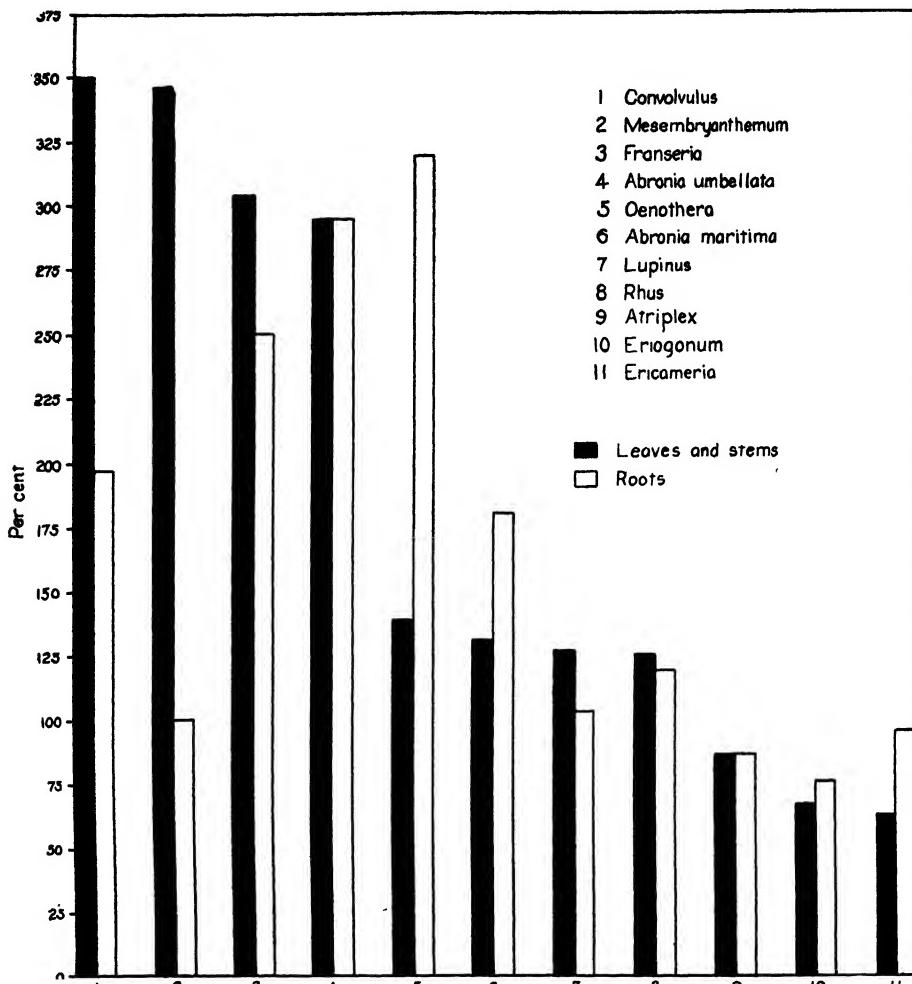
FIG. 7. Percentages of water in leaves and stems compared with roots of eleven dune species (calculated on the dry weight basis).

The method used by the writer, which may be called the direct method, was an attempt to ascertain whether a water deficit existed in any of the eleven species during August, 1932. If a deficiency existed in any plant, and water was available through the aerial portions, it might be absorbed through this channel since it was not available through the usual agent of absorption, the root system. The quantity absorbed per unit of surface was not determined.

At the time of the experiment the plants at both El Segundo and on the Silver Strand had received no moisture in the form of rain for over 3 months. The procedure was as follows: Into quart bottles of distilled water in which 100 mg. of eosin had been dissolved, there were immersed healthy branches

attached to the plants growing in their habitat, care being taken not to use mutilated or cut leaves or stems. A thin film of oil was placed over the surface of the water to prevent evaporation, and a file mark on the neck of the bottle indicated the water level. After several tests a period of 24 hours was decided upon as being the most suitable, at the expiration of which the amount of water withdrawn was determined. The specimens were then removed to the laboratory, dried and sectioned.

A water deficit was apparent in each of the eleven species in August, 1932, otherwise they would not have absorbed water through their aerial parts.

ROOT SYSTEMS

These may be conveniently grouped into systems with (1) well-developed main root, as in *Abronia umbellata*, (2) those with both main root and laterals well developed, as in Rhus, and (3) those with short roots superficially placed, as in Mesembryanthemum. Almost all the systems excavated showed, however, a considerable depth as compared with the height of the aerial parts of the plant. A few of the tap-roots were fleshy, as in Franseria, while Convolvulus had a well developed rhizome habit. No bulbous plants were found. The data gathered agree with Cannon's (1924) observation in South Africa. He says:

The sclerophyllous species all appear to have roots which vary to a certain and possibly usually considerable degree as regards the depth and lateral extent of development, but they all agree on having relatively large development of the root-systems.

The succulent habit, as a rule, is accompanied by a meager root-system. After a heavy rain with practically no run-off, the sand surface soon dries by evaporation, the soil below maintaining its moisture for some time partly because the upper layer of dry sand reduces capillary action. Moisture by its retention in the plant body is available for use in succulents long after the rains cease. In the dunes, when the plant possesses little or no succulence, the depth of the root system increases.

Root length may be influenced, however, by other conditions than the amount of soil water. Cannon (1925) states that the branching of roots occurs whenever there is sufficient oxygen in the soil to permit root-growth. Waterman (1919) in his work on root systems of Lake Michigan sand dune plants from the viewpoint of their development, finds that their reactions are specific and hereditary. He believes that the evidence points conclusively to nutrient, or at least to chemical influences, as the cause of variability in symmetry of root extension under dune conditions. In the present investigation there is a noticeable variability in the form and the development of the root system of each species. Weaver (1919) finds that plains species under dune conditions develop roots of less depth than such species not growing in dunes.

Aside from these influences, others may be the chemical composition of the soil and the soil temperature.

Because the substratum in much of the dune area is of a shifting nature, plants growing there must be able to accommodate themselves to this instability if they are to grow there at all. One means by which this instability is withstood is the production of adventitious roots on stems when these are buried by sand. Many species are rooted deeply enough to attain a moist soil layer that remains moist all through the long dry season. *Abronia maritima* is the principal pioneer and dune former, while Franseria is a stabilizer of flat surfaces. Rhus has its lower branches procumbent, these sometimes taking root at the nodes. Adjustments, in other words, are made in different ways.

ANATOMY OF THE STEM

The stems may be placed conveniently in two groups, namely, those which have much water accumulative and little mechanical tissue, and those which are woody. The cortical parenchyma of the Abronias and Mesembryanthemum constitutes a wide band composed of water accumulative tissue. The woody stems, on the other hand, have a narrow cortex and an extensive development of xylem, as in Ericameria. Those with water accumulative tissue usually have a large proportion of pith; woody stems have a small amount, even when young.

There is considerable variation in the epidermal covering. Most of the young stems possess a layer of cuticle. While Mesembryanthemum and Convolvulus have a smooth epidermis, *Abronia maritima* and *A. umbellata* bear glandular trichomes. Young stems of Eriogonum, on the other hand, have both glandular and non-glandular trichomes, while only the non-glandular occur in Ericameria, Franseria, Lupinus, Oenothera and Rhus. Atriplex bears vesicular trichomes. The frequency of such outgrowths varies from a scattering to a dense covering, giving a silvery appearance to the stems of some species. Older stems of the woody forms develop a suberized layer. Anomalous structure occurs in the vascular tissue of *Abronia maritima, A. umbellata,* Atriplex, and Mesembryanthemum, where a ring of cambium has developed concentric circles of xylem separated by parenchyma. These are probably genetic variations.

The percentage of the stem devoted to tracheids and tracheae, and the relative proportion of each, vary with the age of the individual as well as with the species itself. The Abronias, Atriplex, and Convolvulus contain a small number of tracheae. In Mesembryanthemum they are exceedingly small in size as well. The phloem always constitutes a very small portion of the vascular bundle, being on the outside of it except in Convolvulus where the bundles are bicollateral.

Anthocyanin is present in, or just below, the epidermal layer in *Abronia*

umbellata, Atriplex, Franseria, Convolvulus, Mesembryanthemum, Oenothera, and Rhus.

Crystals of various types commonly occur in the cortical or pith parenchyma. The most usual form is that of bundles of raphides, as in *Abronia maritima, A. umbellata,* Mesembryanthemum, Oenothera; acicular crystals are found in Ericameria and druses in Atriplex, Franseria, Eriogonum and Rhus. In Convolvulus and Lupinus none were in evidence during the investigation.

Mechanical tissues, in the forms of sclerenchyma and collenchyma are, of course, present in many of the stems. Rhus has sclerenchyma in the form of arcs around each resin duct of the phloem portion of the vascular bundles. In plants with anomalous structure, *Abronia maritima, A. umbellata,* and Mesembryanthemum, the unusual disposition of xylem instead of distinctively mechanical tissue apparently provides sufficient support.

Stomata are not numerous in the stems of any of the herbaceous species; some are slightly sunken.

In the stems of all eleven species intercellular spaces are noticeably small in size and reduced in number.

Chloroplasts are diversely dispersed in the cortical parenchyma. In some species, as in *Abronia maritima* and Mesembryanthemum, they are distributed throughout this parenchyma, while in others, as in *Abronia umbellata,* they occur irregularly in the few rows of parenchyma immediately beneath the epidermis, or, again, as in Atriplex, they are in cells arranged in small groups in the cortex.

TABLE 9. Summary of structural features of the stem.[17]

Species	Succulent	Suffrutescent	Woody	Tracheae		Tracheids		Water accumulative tissue		Collenchyma	Sclerenchyma	Inclusions		
				Numerous	Few	Numerous	Few	Present	None			Crystals	Latex	Resin
Abronia maritima.....	x[18]	.	.	.	x	.	x	x	.	.	.	x	.	.
Abronia umbellata....	x	.	.	.	x	.	x	x	.	.	.	x	.	.
Atriplex........	.	x	.	.	x	.	x	x[19]	.	x	.	x	.	.
Convolvulus....	x	.	.	.	x	.	x	x	.	.	.	x	x	.
Ericameria.....	.	.	x	x	.	.	x	.	x	.	x	x	.	x
Eriogonum.....	.	.	x	.	x	x	.	.	x	.	x	x	.	.
Franseria.......	.	x	.	.	x	.	x	x[19]	.	.	.	x	.	.
Lupinus........	.	.	x	.	x	x	.	.	x	.	x	.	.	.
Mesembryanthemum......	x	.	.	.	x	.	x	x[19]	.	.	.	x	.	.
Oenothera......	.	x	.	.	x	x	.	.	x	x	.	x	.	.
Rhus..........	.	.	x	.	x	x	.	.	x	x	x	x	.	x

[17] Data gathered from El Segundo, Los Angeles County, and Silver Strand, San Diego County, from September, 1931 to January, 1933.
[18] "x" Denotes presence of the characteristic.   [19] When young.

ANATOMY OF THE LEAF

Of all plant organs the leaf is most responsive to changes in environmental conditions, and in sand dune vegetation leaves have become modified in several different ways. Although much of the sand dunes is xero-mesic rather than xeric, plant responses to the peculiar edaphic conditions are decidedly xeric in character. Many of the leaves bear trichomes; closely placed, unbranched, uniseriate ones predominating. They are especially abundant in Franseria and Lupinus, where they are present on both surfaces. In the Abronias the trichomes are glandular, being more abundant in *A. maritima.* Eriogonum has both glandular and non-glandular sorts. In Rhus only unicellular, unbranched forms of scattered occurrence are present, while in Convolvulus and Mesembryanthemum all types are absent. Atriplex is provided with a thick layer of vesicular trichomes; on many dune species, indeed, the trichomal covering is so heavy as to give the leaf a grayish appearance.

Stomata for the most part are small and relatively few in number per unit of surface. They occur in both epidermal layers in *Abronia maritima, A. umbellata,* Atriplex, Convolvulus, Franseria, Lupinus, and Oenothera, on all sides of the needle-like leaves of Ericameria, and on the three sides of the leaf of Mesembryanthemum while on Eriogonum and Rhus they are found in the abaxial alone. Nine of the eleven species have stomata on all sides of the leaf. Frequently subsidiary cells accompany them, as in Mesembryanthemum.

Cuticle is present on all eleven species, but varies considerably in thickness, Atriplex having the thinnest (0.002 mm.) and the adaxial surface of Rhus having the thickest (0.007 mm.).

Epidermal cells are almost uniform on both adaxial and abaxial surfaces, those of the adaxial usually being slightly larger.

The arrangement of the chlorenchyma is an index of the environmental conditions under which sand dune vegetation exists. In some of the species, as in Eriogonum and Lupinus, the mesophyll is composed largely of palisade. This is advantageous, since a leaf of this type transpires less than one whose mesophyll consists of spongy tissue alone. Other species, as the Abronias and Franseria, have palisade at either side of the leaf, being of the diplophyll type, except that sometimes the spongy mesophyll contains few chloroplasts and becomes in part water-accumulative tissue. In Atriplex the chlorenchyma is removed to the center of the blade, with water accumulative tissue above and below it. In all eleven species the leaf tissues are very compact, the degree of this compactness determining to some extent the transpiration.

One of the most striking features of many of the sand dune plants is the abundance of water accumulative tissue. Its position varies in that it may be distributed throughout the mesophyll, as in *Abronia maritima;* in the center of the mesophyll near the veins, as in Convolvulvus, or it may be peripheral,

as under the epidermal surfaces in Atriplex. When the leaves of some of the species become older, they thicken, and much of this thickening is due to an increase in the amount of water accumulative tissue. This is well shown in *Abronia maritima*, where in some cases the cells which were cholorophyll-bearing in the young leaf become enlarged, the chloroplasts disappear, and the cells become wholly storage in function. Water accumulative tissue occurs in seven of the eleven species, namely, in *Abronia maritima, A. umbellata,* Atriplex, Convolvulus, Franseria, Mesembryanthemum, and Oenothera. Eighty per cent of the species investigated by Kienholz (1926) had some form of water storage tissue, while Harshberger (1909) listed 20 per cent of his New Jersey sand-strand species as succulent.

Crystals of various types occur in the mesophyll, the most common form, that of bundles of raphides, being present in *Abronia maritima, A. umbellata* and Mesembryanthemum. Acicular crystals are found in Convolvulus and Ericameria and druses in Atriplex, Eriogonum, Franseria and Rhus. No crystals were observed in the leaves of Lupinus during the investigation, and were, therefore, present in ten of the eleven species. Latex was found in Convolvulus, resin in Rhus, and mucilage in Mesembryanthemum. Anthocyanin is of general occurrence in the sand dune plants, although found in the leaves of but four of the species investigated, namely, in Convolvulus, *Abronia umbellata,* Mesembryanthemum and Rhus.

Variation in leaf structure within the same species is most evident in the differing proportions of water accumulative tissue in *Abronia maritima,* Con-

TABLE 10. Summary of structural features of the leaf.[20]

Species	Leaf			Trichomes		Palisade				Sponge		Stomata		Inclusions			
	Microphyll	Succulent	Broad sclerophyll	Both surfaces	Abaxial only	Throughout	All surfaces	Adaxial	Center	Present	None	Both surfaces	Abaxial only	Crystals	Latex	Mucilage	Resin
Abronia maritima....	.	x[21]	.	x	.	.	x	.	.	x	.	x	.	x	.	.	.
Abronia umbellata...	.	x	.	x	.	.	x	.	.	x	.	x	.	x	.	.	.
Atriplex......	.	x	.	x	.	.	.	.	x	x	.	x	.	x	.	.	.
Convolvulus...	.	x	.	.	.	.	x	.	.	x	.	x	.	x	x	.	.
Ericameria....	x	.	.	.	.	.	x	.	.	x	.	x	.	x	.	.	x
Eriogonum....	.	.	.	.	x	.	x	.	.	x	.	.	x	x	.	.	.
Franseria.....	.	x	.	x	.	.	x	.	.	x	.	x	.	x	.	.	.
Lupinus......	.	.	.	x	.	x	.	.	.	.	x	x	.	.	.	.	.
Mesembryanthemum....	.	x	.	.	.	.	x	.	.	x	.	x	.	x	.	x	.
Oenothera....	.	x	.	x	.	.	.	x	.	x	.	x	.	x	.	.	.
Rhus........	.	.	x	.	x	.	.	x	.	x	.	.	x	x	.	.	x

[20]Data gathered from El Segundo, Los Angeles County, and Silver Strand, San Diego County, from September, 1931 to January, 1933.
[21]"x" Denotes the presence of the characteristic.

volvulus, and Franseria, an increase of this tissue occurring when these species grow near the strand. In Rhus the number of palisade layers varies from two to three on the adaxial surface.

ANATOMY OF THE ROOT

There is not so much variability here as in the aerial parts. A large cortical parenchyma, with a tendency toward succulence, is found in *Abronia maritima, A. umbellata* and Franseria. Convolvulus and Mesembryanthemum, with fibrous roots, have a cortical parenchyma that is very large in proportion to the stele. In Ericameria, Eriogonum, Lupinus, and Rhus, the stele occupies the major portion of the root.

Pith parenchyma rarely occurs; *Abronia maritima,* however, has a rather large area of it. Franseria has its pith cells lignified, while in Atriplex, Lupinus, Eriogonum, Ericameria, and Rhus, xylem and not pith occupies the center of the root. Ericameria and Rhus have a considerable development of cork.

Sclerenchyma is developed in Eriogonum. Starr (1912) found that roots of sand dune plants are generally sclerenchymatous, with collenchyma in the cortex. In the present investigation both were apparently but little developed.

Anomalous structure, in which there are successive rings of cambium producing vascular bundles separated by parenchyma, was found in *Abronia maritima, A. umbellata,* Atriplex and Mesembryanthemum.

Crystals are present, principally in the cortical parenchyma, appearing in their most common form, that of bundles of raphides, in *Abronia maritima, A. umbellata,* and Mesembryanthemum. No crystals were found during the

TABLE 11. Summary of structural features of the root.[22]

Species	Fibrous	Woody	Tracheae		Tracheids		Sclerenchyma	Inclusions		
			Numerous	Few	Numerous	Few		Crystals	Latex	Resin
Abronia maritima...	.	x[23]	.	x	.	x	.	x	.	.
Abronia umbellata...	.	x	.	x	.	x	.	x	.	.
Atriplex............	.	x	x	.	x	.	.	.	.	.
Convolvulus........	x	.	.	x	.	x	.	.	x	.
Ericameria.........	.	x	.	x	x	.	.	.	.	x
Eriogonum.........	.	x	.	x	x	.	x	.	.	.
Franseria..........	.	x	.	x	x	.	.	.	.	x
Lupinus............	.	x	.	x	x	.	.	.	.	.
Mesembryanthemum.	x	.	.	x	x	.	.	x	.	.
Oenothera..........	.	x	x	.	x	.	.	.	.	.
Rhus..............	.	x	x	.	x	.	.	.	.	x

[22] Data gathered from El Segundo, Los Angeles County, and from Silver Strand, San Diego County, from September, 1931 to January, 1933.
[23] "x" Denotes the presence of the characteristic.

investigation in Atriplex, Convolvulus, Ericameria, Eriogonum, Franseria, Lupinus, Oenothera, and Rhus. Resin is present in Franseria and Rhus and latex in Convolvulus.

CORRELATIONS OF ENVIRONMENTAL CONDITIONS AND VEGETATION

TEMPERATURE AND PRECIPITATION AS AFFECTING ALL THE STATIONS

The temperature of the air in these areas is on the whole uniform and moderate. It seldom drops to the freezing point during winter, but even when this does occur, the point of a killing frost is not reached except at very infrequent intervals (Clements, 1916). A marked feature of the Mediterranean type of climate, which is that generally prevalent in southern California, is the non-accordance of favorable temperatures with the rainy season. The El Segundo dune area lies in the "steppe climate" (BShs—dry climate; steppe; hot type; winter precipitation), and the Silver Strand dune area in his "foggy desert climate" (BWhns—dry climate; desert; hot type; foggy summer; winter precipitation) of the Russell (1931) modification of the Köppen international system. The precipitation is somewhat meager, varying considerably from year to year. Ninety per cent falls in the 6 months from November to the end of April, based on the records of the U. S. Weather Bureau stations at San Diego for the past 81 years and at Los Angeles for the past 54 years. In the 3 months, August to November, preceding this period, there is a small amount of precipitation, about 0.59 inch or 6.0 per cent of the annual total at San Diego, and about 0.83 inch or 5.5 per cent at Los Angeles. As this comes after several rainless months, it is practically unavailable to the vegetation growing in a soil already depleted of water. From December to March, when, owing to the low air and soil temperatures, the metabolism of the plant is reduced, soil moisture is abundant and the evaporating power of the air low. In spring the temperature becomes favorable for metabolism, but as the season advances the soil moisture becomes depleted and evaporation increases. Summer and autumn, therefore, are the unfavorable periods.

The vegetation of the dunes has become modified in different ways to meet these conditions. One group of plants, represented by Mesembryanthemum, grows rapidly in early spring when soil moisture is ample and temperatures are becoming favorable, accumulating water for its slow growth during the summer and the autumn. From monthly measurements of twelve stems, Mesembryanthemum grew approximately 2.5 cm. in length per month from August to November, 1932. This appears to be an excellent rate of growth for the unfavorable period of late summer and autumn. From July to November of that year, the rainfall amounted to but 1.4 inches. The soil

moisture at the roots of these plants at this time was about 0.5 per cent, so small an amount that it was probably unavailable to the plant, even if high osmotic pressure was maintained. Conservation of moisture in the plant is aided by a thick layer of cuticle and by embedded stomata.

The second group of plants is suffrutescent. The herbaceous portions of the stems largely die back during the dry season, as in Oenothera. With lessened shoot system during summer, the plant appears to contain sufficient water even though its roots are not deep enough to attain moist soil. Moisture, such as dew, may be absorbed through its aerial portions.

A third group of plants, the shrubs, such as Lupinus, Ericameria and Rhus, probably do not have so great a water deficit as those in the previous groups, since the shrubs have deeply penetrating root systems extending to moist soil layers at all seasons. In addition to this, each of these species has modifications for lessening water loss. Water, however, is not available so soon to the shrubs as to the shallow-rooted succulents, since the early autumn rains are often light and moisten only the surface layers of the soil.

Evaporation and Other Environmental Influences at Each Station

The severest environmental conditions throughout the year are encountered in the moving dunes, in which location Franseria is most frequently found. The most noticeable features of this environment are the instability of the substratum, the intensity of the light, the high evaporation rates, both higher and lower soil temperatures, less soil moisture, and soil of a coarser texture than in any other dune locality. Franseria, with its fleshy tap-root, can withstand partial covering by sand and can make rapid growth. Of the six stations maintained, the moving dune station consistently showed the highest rates of evaporation, almost twice as much as those at any other station. Here higher wind velocity and greater light intensity prevail. Franseria is modified to meet these adverse environmental conditions. Its habit of growth is low and spreading, serving for sand stabilization. With the succulence of its tap-root, and, in addition, with that of its stems and leaves when the plant is growing near the strand, it accumulates rather more water than is superficially apparent. The surfaces of the leaves and younger stems are covered with trichomes. The crystals, present in most of its tissues, probably aid in the concentrating of the cell sap. In the moving dunes the percentage of soil moisture is very low during the summer months; at a depth of 10 cm. less than 0.5 per cent was found monthly in the period of 6 months from May to November, 1932. The roots of Franseria, while penetrating below 10 cm., lie mainly in a layer of soil that has about 1.0 per cent of moisture. The amount of water available from the soil during the summer

period is probably insufficient for the species.[24]   Franseria, no doubt, uses its accumulated water.

Next to the moving dunes, the greatest evaporation rates occur near the strand.   Here are located *Abronia maritima,* Atriplex, and occasionally Franseria, all of which hold the sand in small foredunes.   The soil hereabouts is somewhat more stable, because it is not yet sufficiently dry to be actively blown about, as is the case in areas more removed from the ocean where moving dunes are found.   Light intensity is great.   There is probably somewhat less wind affecting vegetation here, since the plants lie close to the ground, and are, besides, seldom elevated by means of sand mounds, as happens farther back.   There is not so great fluctuation in soil temperature in this area as at the moving dune station, while the soil moisture is greater during the drier portions of the year.   The plants of this environment, with succulence their chief characteristic, are in a location where they are at times subject to a deposition of salt spray.   Water accumulative tissue is present in the cortical parenchyma of the stems, and sometimes in the roots, of *Abronia maritima* and Atriplex.   *Abronia maritima* develops water accumulative tissue somewhat variously in the mesophyll.   The cells of the chlorenchyma become enlarged, some of the chloroplasts disappear as such, and the cells are water accumulative in addition to retaining the photosynthetic function in part. Atriplex has its water accumulative tissue located in definite layers inside of either epidermal surface, a position of this tissue which serves to protect the underlying tissues against excessive light.   Both species have their leaf and stem surfaces covered with closely overlapping trichomes, those of Abronia being glandular while those of Atriplex are vesicular.

At a depth of 10.0 cm., soil moisture, calculated on the dry weight of the soil, ranged between 0.25 and 0.51 per cent for the period of greatest dryness, the six months May to November, 1932.   At 20 cm. depth, it averaged less than 1.0 per cent, and below the latter depth, where roots of Abronia and Atriplex occur, the percentage varied, but was slightly over 1.00 per cent for most of the period mentioned.   The species may be able, through the concentration of their cell sap, to secure water, although the amount available must be small.

Near the strand two succulents, Mesembryanthemum and Convolvulus, are found.   Mesembryanthemum, with its fleshy equilateral leaves, is the most succulent species of the dunes.   Both plants are of low growth habit, Convolvulus spreading by means of rhizomes and Mesembryanthemum by its prostrate aerial stems which root at the nodes.   Leaves of both species are covered with a thick layer of cuticle, and the mesophyll is compact, that of Mesembryanthemum being largely of water accumulative tissue.   Stomata are present on both surfaces of Convolvulus and on all three sides of the tri-

[24] Kearney (1904), states that a test of soil at Long Beach, Calif., made in September, showed much less water at the time of examination than is usually the case on the Atlantic coast.

angular leaf of Mesembryanthemum, where their frequency no doubt permits considerable transpiration. In the latter species, however, the stomata are depressed in the epidermal layer and protected by an over-hang of the subsidiary cells. Sclereids in the palisade tissue of Mesembryanthemum prevent collapse when turgor is reduced. Mucilage is present in Mesembryanthemum; latex in Convolvulus.

It was observed that Franseria and *Abronia maritima* just back of the strand were much more succulent with larger and thicker leaves than farther inland. Measurements of 50 leaves of Abronia at Guadalupe, Santa Barbara County, close to the strand, showed an average thickness of 5.5 mm.; farther inland, the average was 2.7 mm. Leaves of Franseria were not only thicker but also less pinnatifid. Both species were thriving in either location, their succulence nearer the strand being probably an indication of more xeric conditions there.

Near the strand in an excavation to a depth of 2.5 feet, which was a few inches below the roots of an *Abronia maritima* specimen, the soil showed a slight saltiness.[25]

Species near the strand do not develop root systems as deep as those in the dune complex. Of the strand plants *Abronia maritima* and Atriplex are not deeply rooted. Farther inland Convolvulus has the rhizome habit with a small development of roots. Still farther inland the plants are deeply rooted, such as the shrubs, Lupinus and Ericameria.

At the dune complex stations at El Segundo, Ericameria (3) and Rhus (4), and at the Silver Strand, Rhus (6), the environmental conditions are more favorable for plant growth than at the three other stations, namely, at El Segundo, moving dune (2), Abronia (1), and at the Silver Strand, Abronia (5). The evaporation at the dune complex stations was less than at the others, the light less intense, and the wind velocity reduced. During most of the period when soil moisture data were obtained the soil of the dune complex stations held a higher percentage of moisture and the soil temperature fluctuated less than at the other stations. The vegetation here, more removed from the ocean than at the other stations, consists largely of shrubs—Ericameria, Lupinus, Eriogonum and Rhus. At station 3 the principal shrubs are Ericameria and Lupinus, the most deeply rooted of all the species investigated. In sites which are partially stabilized the shrubs grow with intervals of several feet between them. The compound leaf of Lupinus has small leaflets which are partly infolded; the leaf in Ericameria is linear and microphyllous. With these reduced leaf areas there are but few stomata. Lupinus bears a close covering of trichomes on both epidermal surfaces. Both the species have cuticle on the epidermises of leaves and young stem, that on the leaves of Ericameria being especially heavy.

[25] Kearney (1904), states that borings at Long Beach, Calif., showed a quite uniform salt content for the first 3 dm. of soil, ranging from 0.12 to 0.15 per cent of water soluble salts.

Environmental conditions are most favorable at the Rhus stations at El Segundo and at the Silver Strand, as compared with the other four stations. Evaporation is consistently less throughout the year at the Silver Strand, with much reduced evaporation rates during the summer months. At El Segundo, during periods when evaporation increases, the increase is less at the Rhus station than at the other three stations, and when it decreases at all stations, it usually decreases but slightly at the Rhus station. In other words, there is less fluctuation at the Rhus station than at the other locations.

Cuticle, especially thick on the adaxial surface, covers the leaves and young stems of Rhus as it does that of Eriogonum, sometimes associated with Rhus. Stomata are present only on the abaxial surfaces, while in Eriogonum this surface is covered by a layer of overlapping trichomes, forming a felt-like covering which cuts down the circulation of air over the leaf and prevents rapid evaporation through the stomata. The leaves of Eriogonum have dense palisade tissue, while in Rhus with two to four rows of palisade, stiffness is supplied by sclerenchyma and collenchyma.

SUMMARY

1. An autecological investigation of the gross morphology and internal anatomy of eleven representative species of the coastal sand dunes of southern California was conducted. Data were obtained of certain important environmental conditions under which the southern California sand dune vegetation grows. An attempt was made to correlate the characteristics and modifications of the species with these conditions of the environment.

2. The southern California coastal sand dunes differ from many such dunes in other areas in that no plants, even if tree species, attain the tree form, the climax appearing to be one of shrubs.

3. Grasses, which are usually a conspicuous feature of sand dune vegetation elsewhere, are scarce in southern California dunes. Aside from *Ammophila arenaria* (L.) Link, which has been introduced, there are no true dune grasses, in as much as those present are typically ruderal or are saline species, such as *Monanthochloe littoralis* Engelm. and *Distichlis spicata* (L.) Greene, which became established in saline locations and upon which sand later accumulated.

4. In plants growing under the xeric dune conditions various structural modifications have developed, such as a sclerophyll type of stiff structure with compact tissues, and a succulent type with a high percentage of water.

5. Differences in the species comprise not only modifications due to variations in the environmental conditions, such as change in the amount of succulence, but also genetic variations, such as growth-form.

6. Plants, such as Franseria, growing in moving dunes and also in more or less level sand areas where the evaporation rates are greatest, exhibit a

low, mostly prostrate growth-form, small leaves, succulent tissue, and a heavy covering of overlapping trichomes on the leaves and stems, giving them a silvery-gray appearance. Their root systems are comparatively shallow.

7. Transition between the more advanced stages of dune vegetation and the chaparral of the inland hills may be indicated by the presence of Rhus. Where this plant occurs are located the more mesic areas of the dunes, in which the evaporation rates are the lowest. It is a shrub, with heavily cutinized, stiff, leathery leaves, with very few trichomes and no succulent tissue.

8. Some species, as *Abronia maritima* and Franseria, when growing near the ocean, bear fleshy leaves, while farther inland the leaves of these plants are less fleshy.

9. Stomatal transpiration appears to be unchecked by any special device in the eleven species, with the possible exception of trichomes.

10. The sand dune plants have a water deficit, at least during certain times of the year, as is shown by their ability to absorb water through their uninjured leaves and stems as they grow in their natural environment.

11. In the littoral of southern California the uniform climate, the rainy season, and, at other times of the year, the moisture from low and high fogs with considerable deposition of dew, make for a fairly low evaporation rate and keep both the air and the soil temperatures favorable for growth during most of the year.

12. The roots are for the most part of normal anatomical structure, being either typically woody as in Eriogonum, Ericameria, Lupinus, and Rhus, or with a somewhat fleshy cortical layer, as in Franseria, Convolvulus, and Oenothera. Anomalous structure is a typical feature of *Abronia maritima, A. umbellata,* Mesembryanthemum and Atriplex.

13. The stems are either of a typical woody type, as in Lupinus, Eriogonum, Ericameria, and Rhus, or succulent, as in *Abronia maritima, A. umbellata,* Convolvulus, Atriplex and Mesembryanthemum.

14. The most pronounced modifications appear in the leaves, ranging from very succulent types, such as Mesembryanthemum and Abronia, to broad sclerophyll, as in Rhus. There are differences in size among the species, though such differences are relatively small. There also occur differences in shape from equilateral to flat and lobed.

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EXPLANATION OF PLATES

All sectional drawings are on a one foot scale.
  (A) Vertical section of plant.
  (a) Surface of the ground.
  (B) Horizontal view of roots.
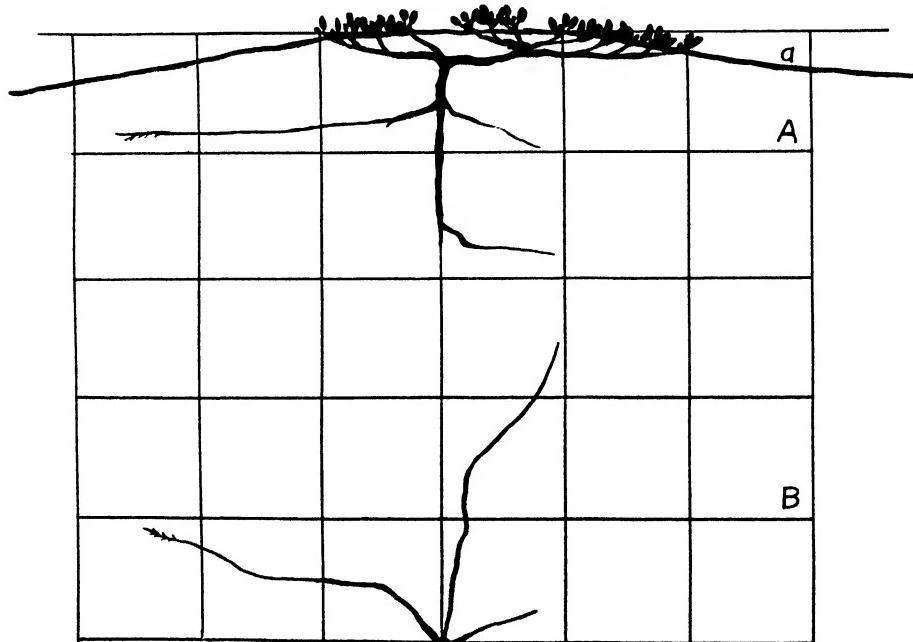
Plate 1. *Abronia maritima* Nutt.
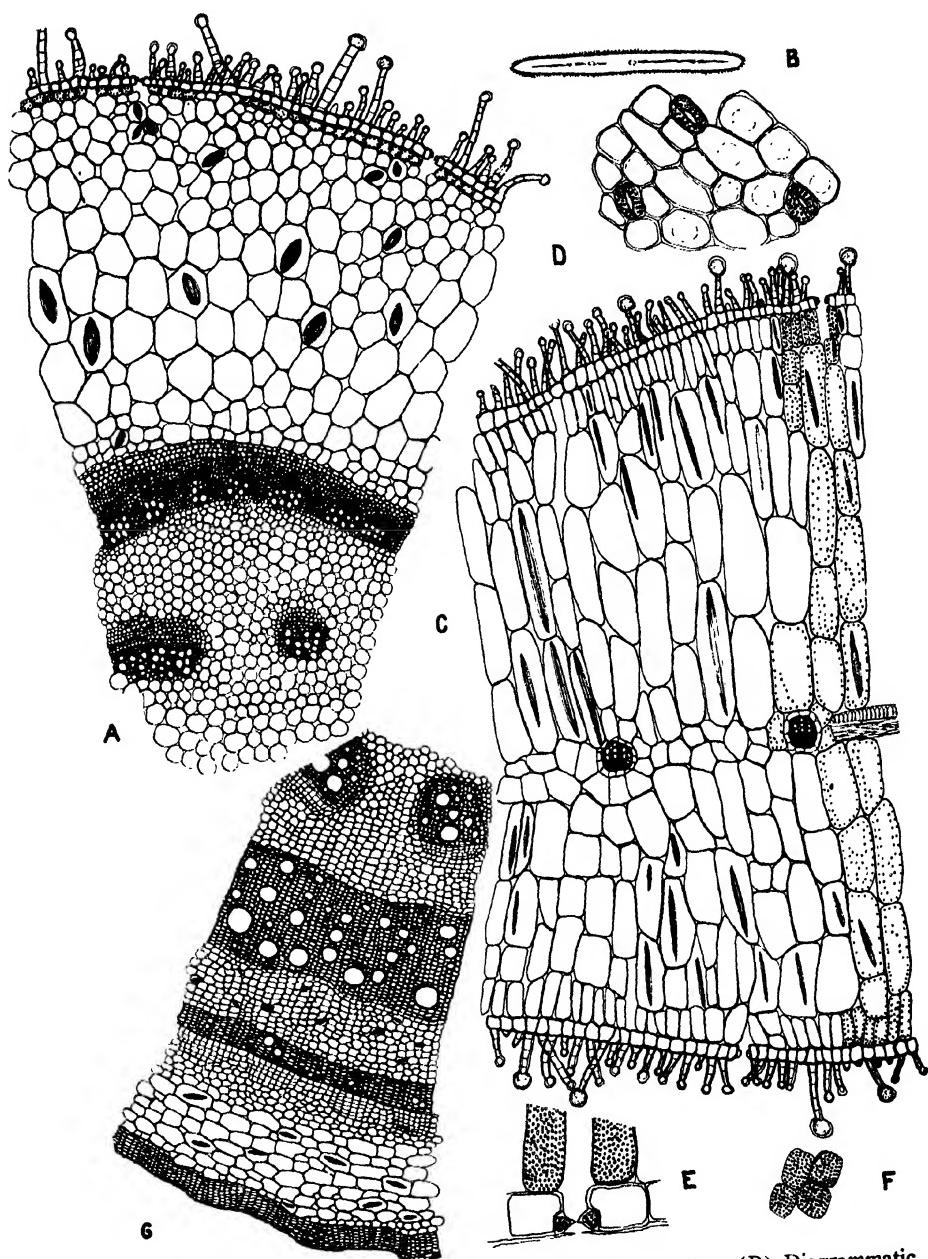
Plate 2. *Abronia maritima* Nutt. (A) Transverse section of stem. (B) Diagrammatic section of leaf. (C) Transverse section of leaf. (D) Epidermal cells showing frequency of stomata. Adaxial and abaxial surfaces are approximately alike. The faint circular lines in some of the cells are the bases of trichomes. (E) Transverse section through epidermal layer showing stoma. (F) Four palisade cells, top view, showing the close placement of chloroplasts. (G) Transverse section of root.
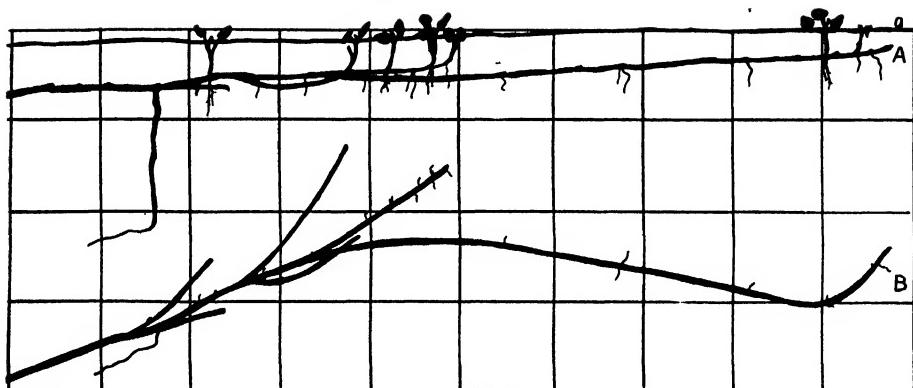
Plate 3. *Convolvulus soldanella* L.
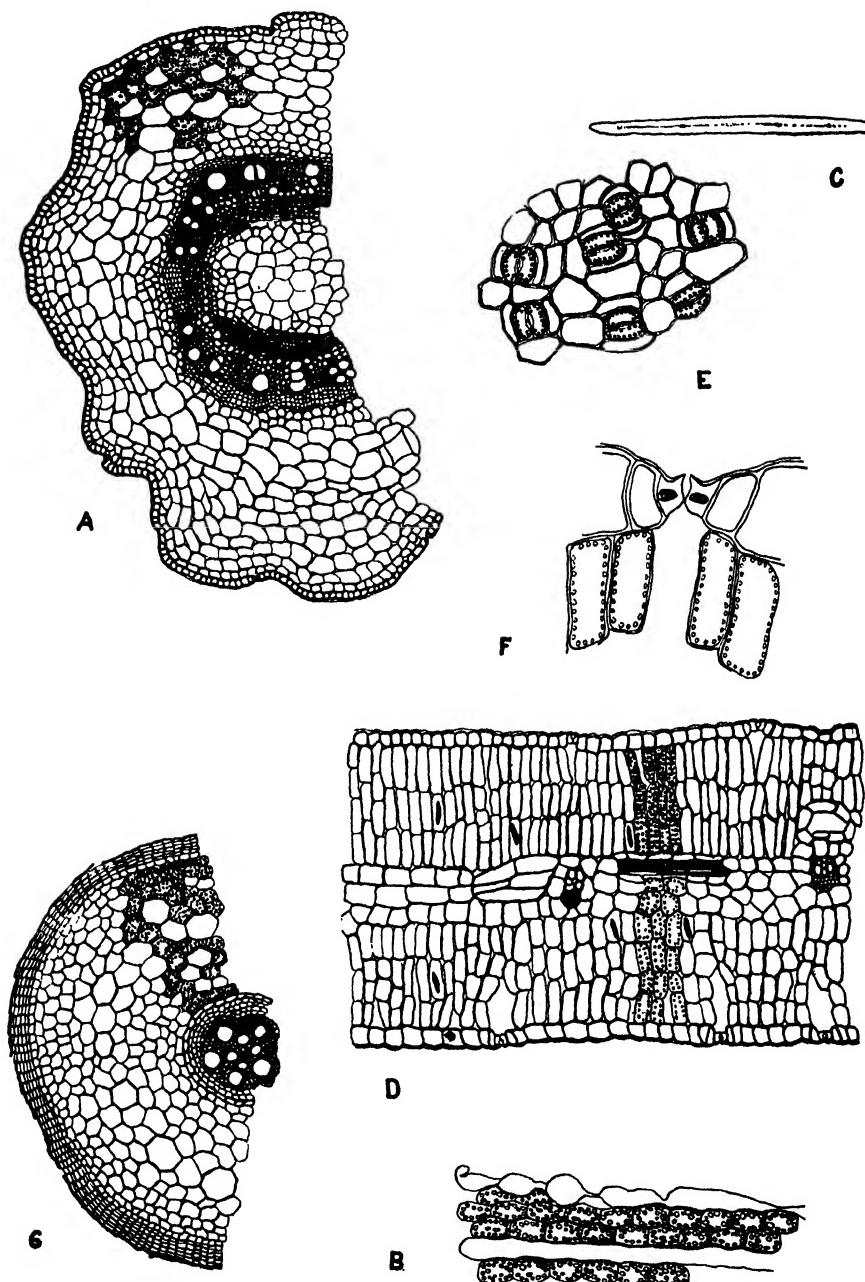
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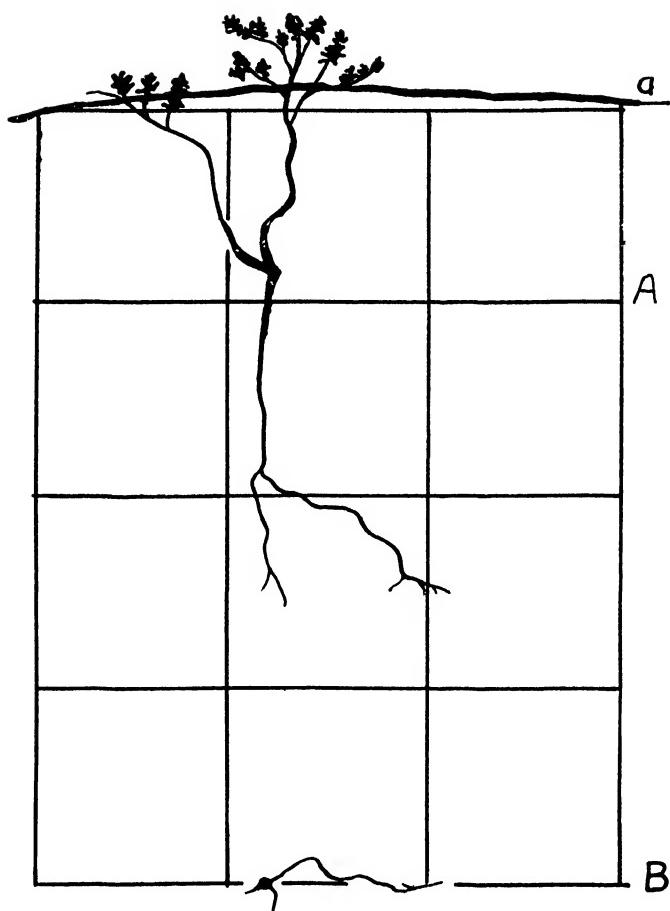
Plate 5. *Atriplex leucophylla* Dietr.
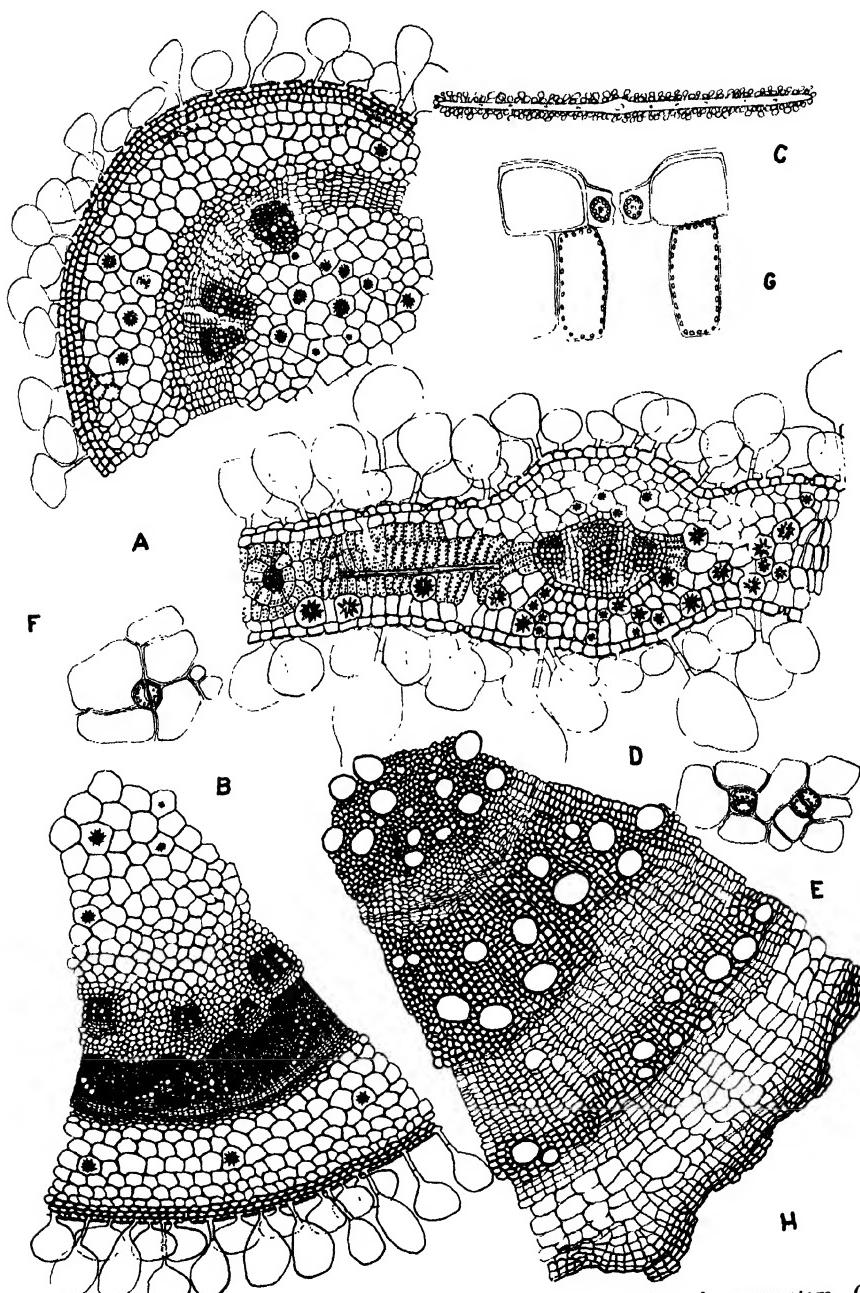
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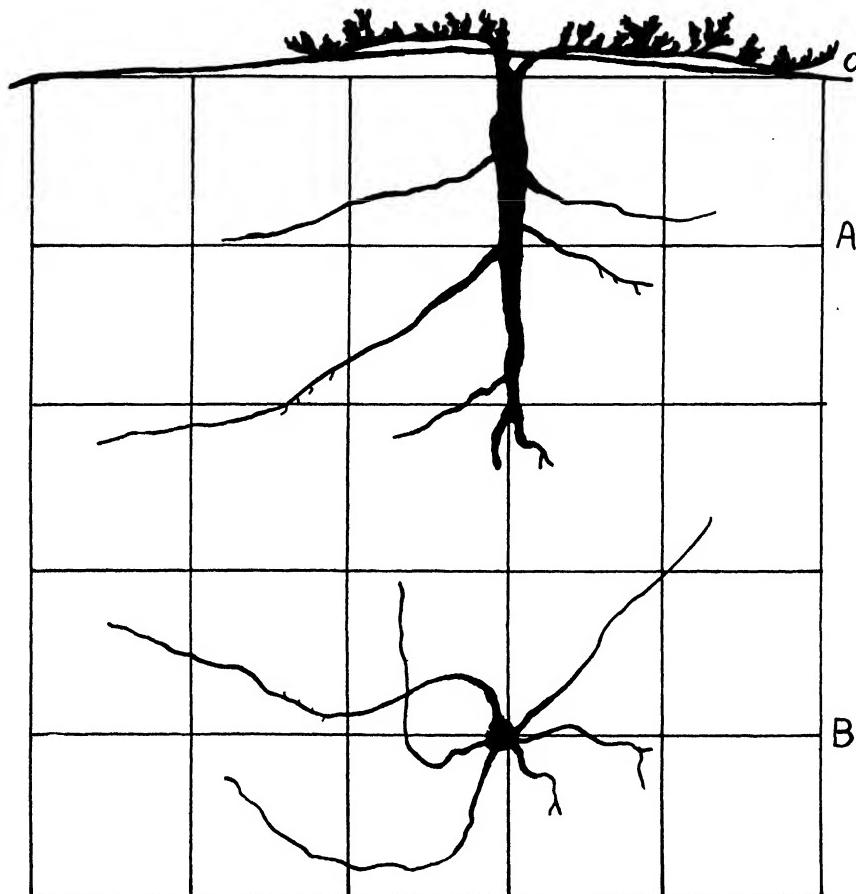
Plate 9. *Franseria bipinnatifida* Nutt.
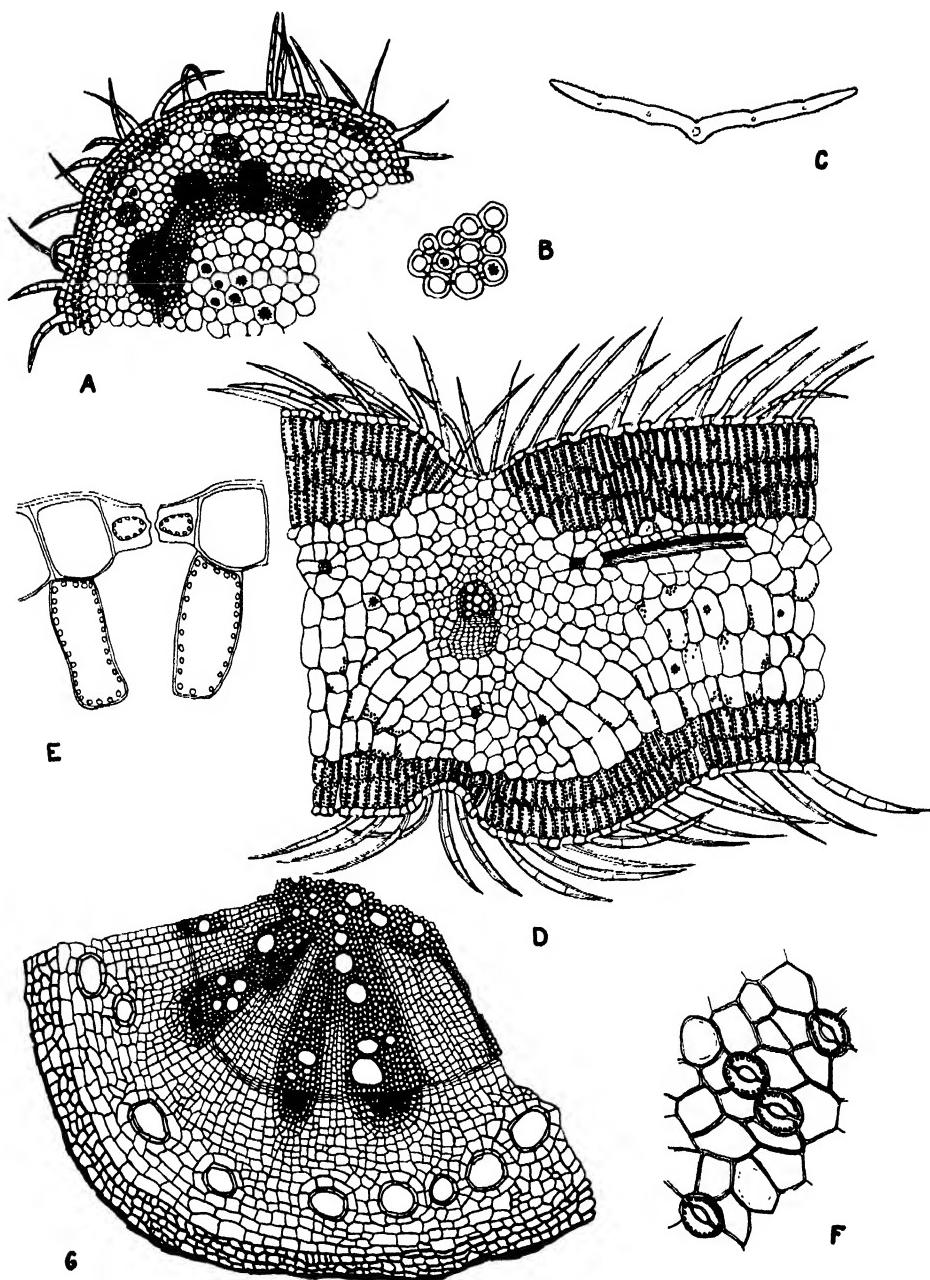
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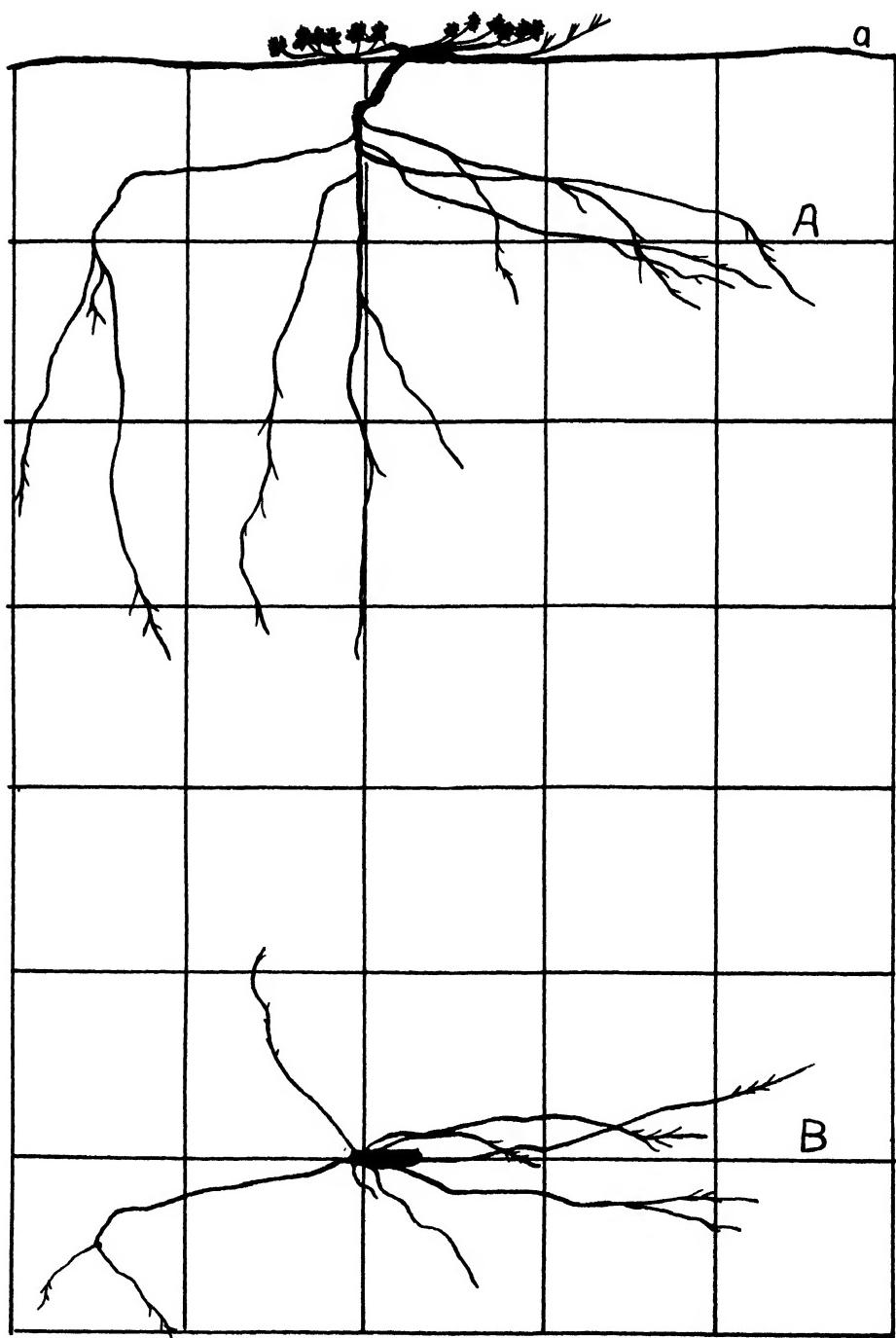
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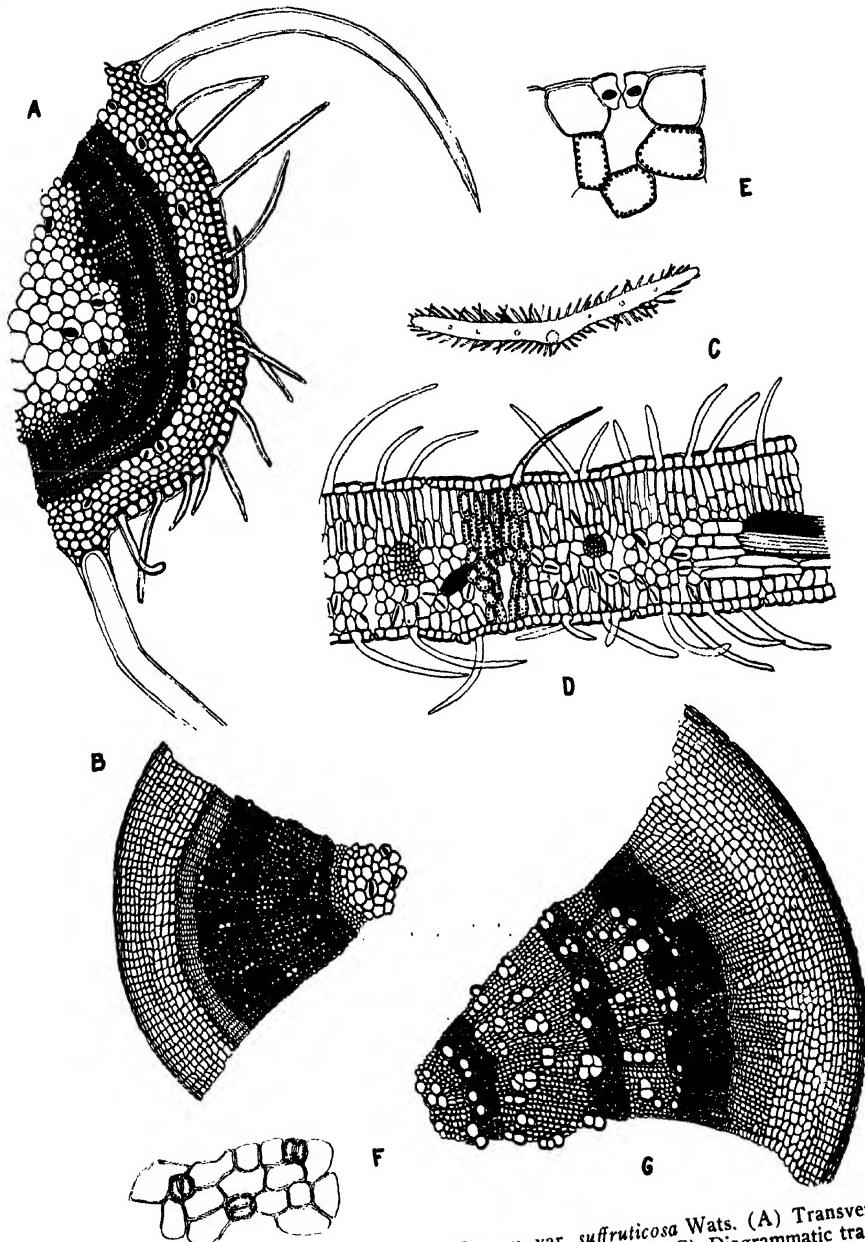
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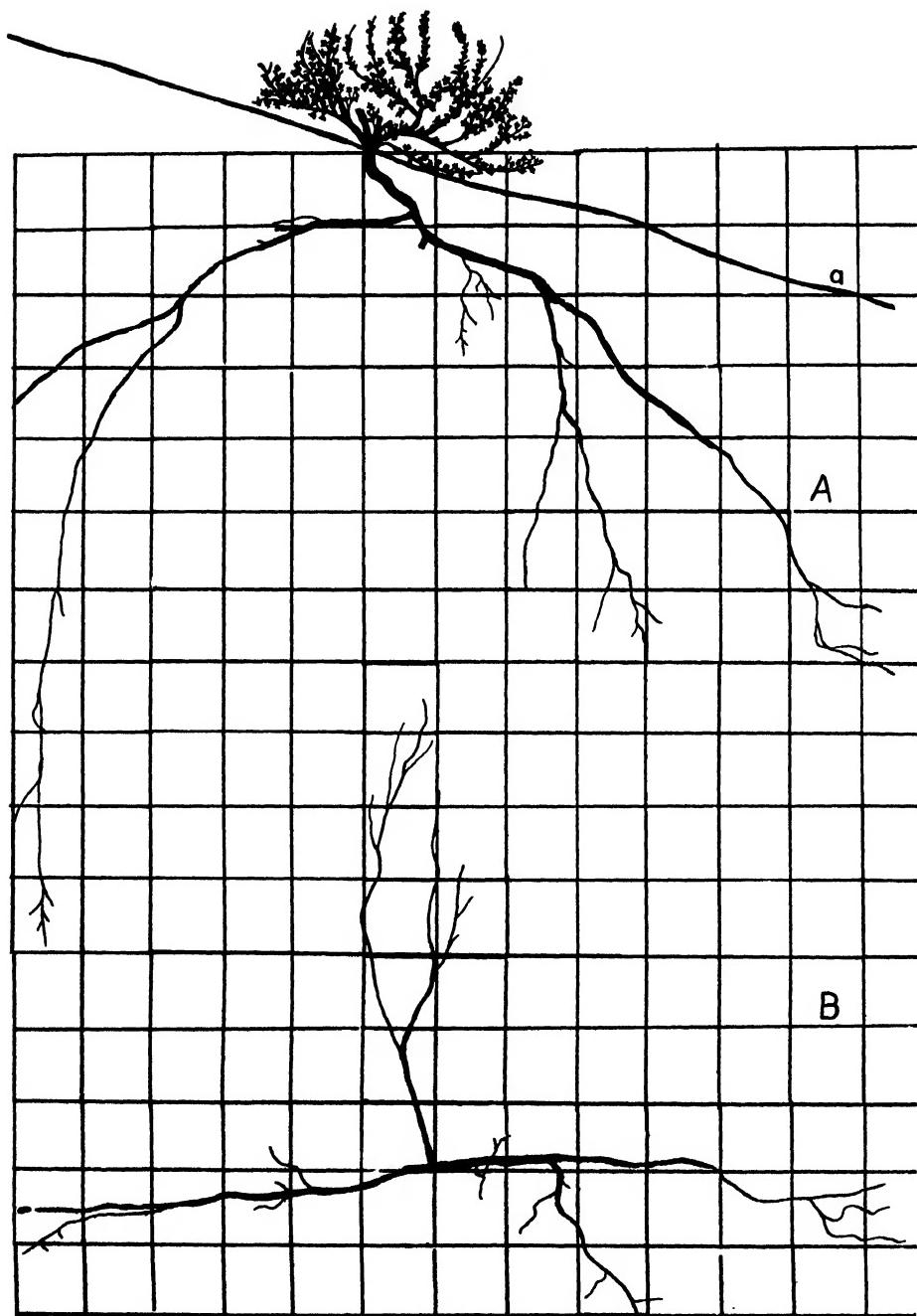
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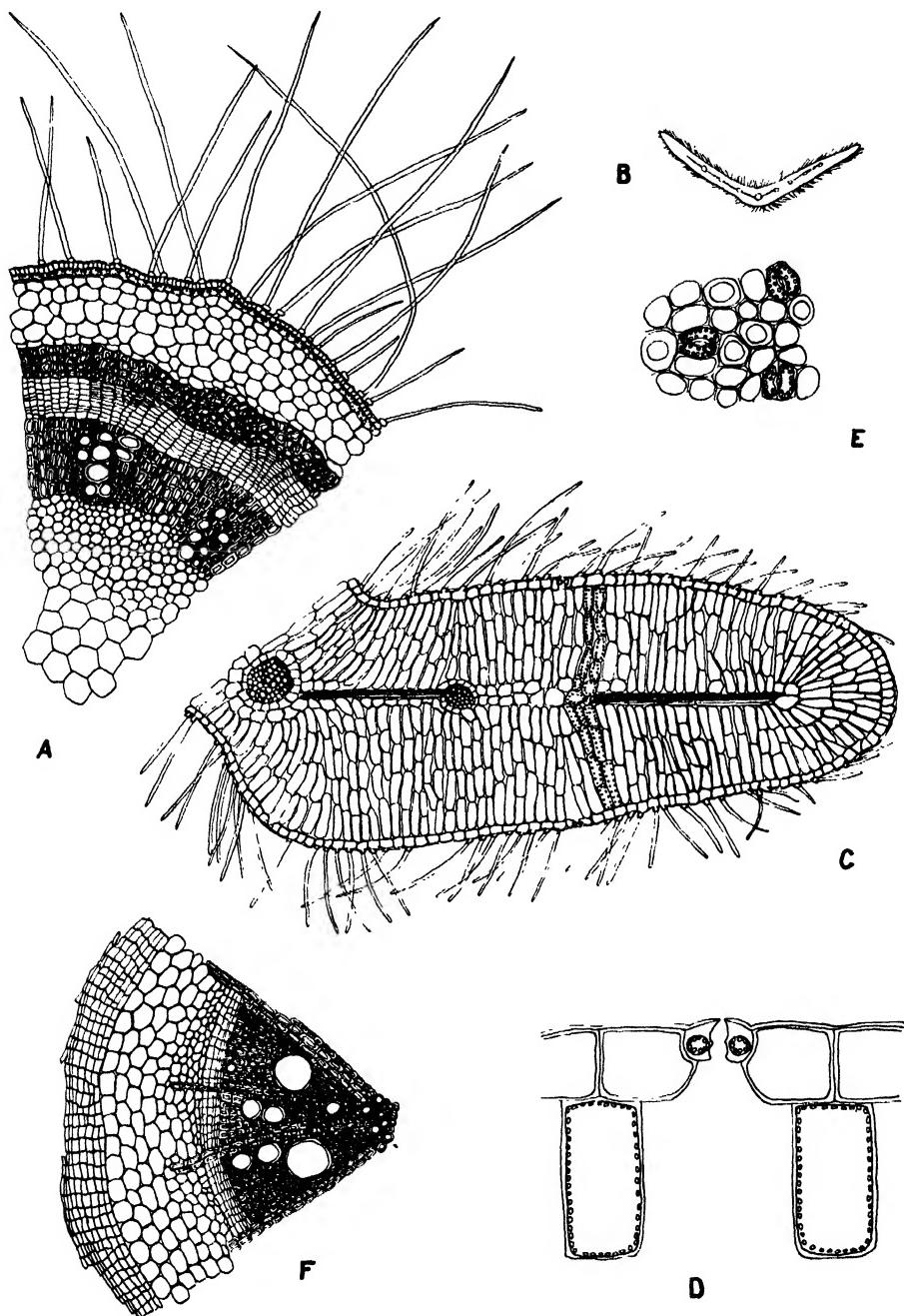
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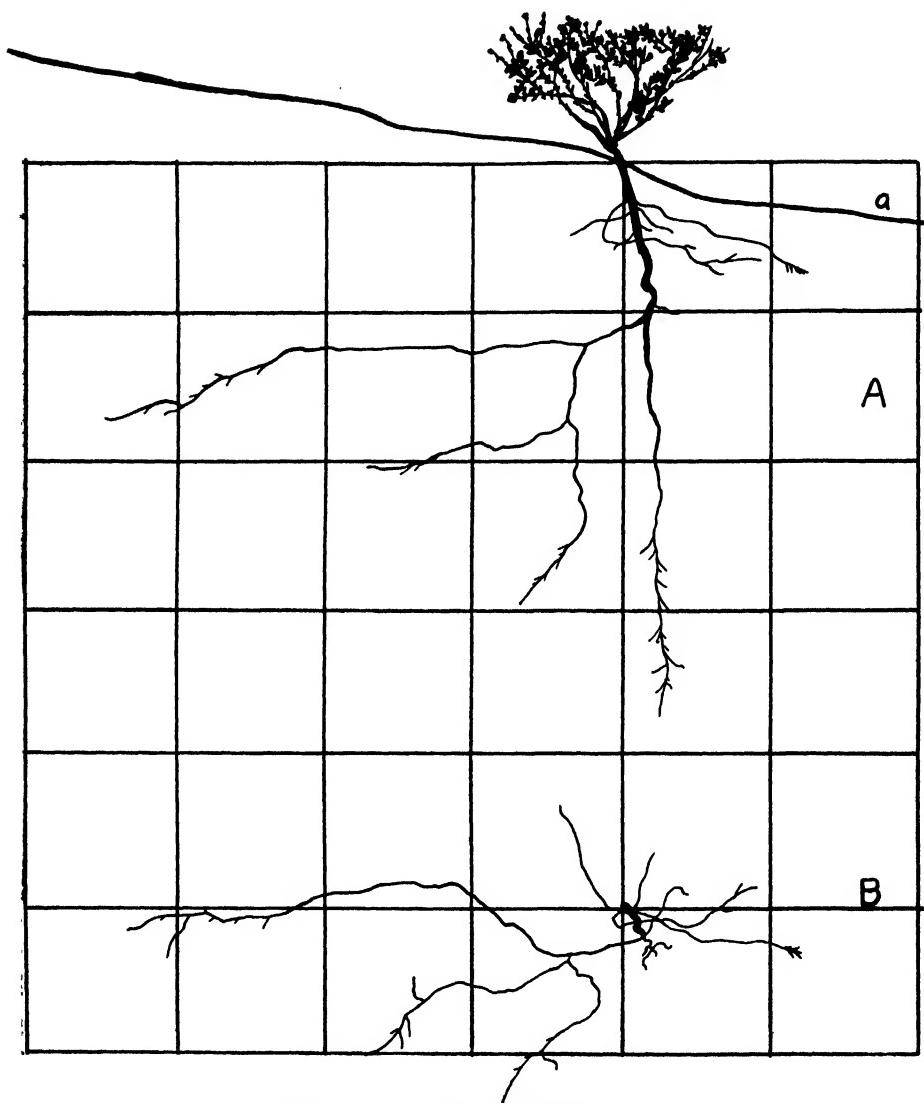
Plate 15. *Eriogonum parvifolium* Sm.
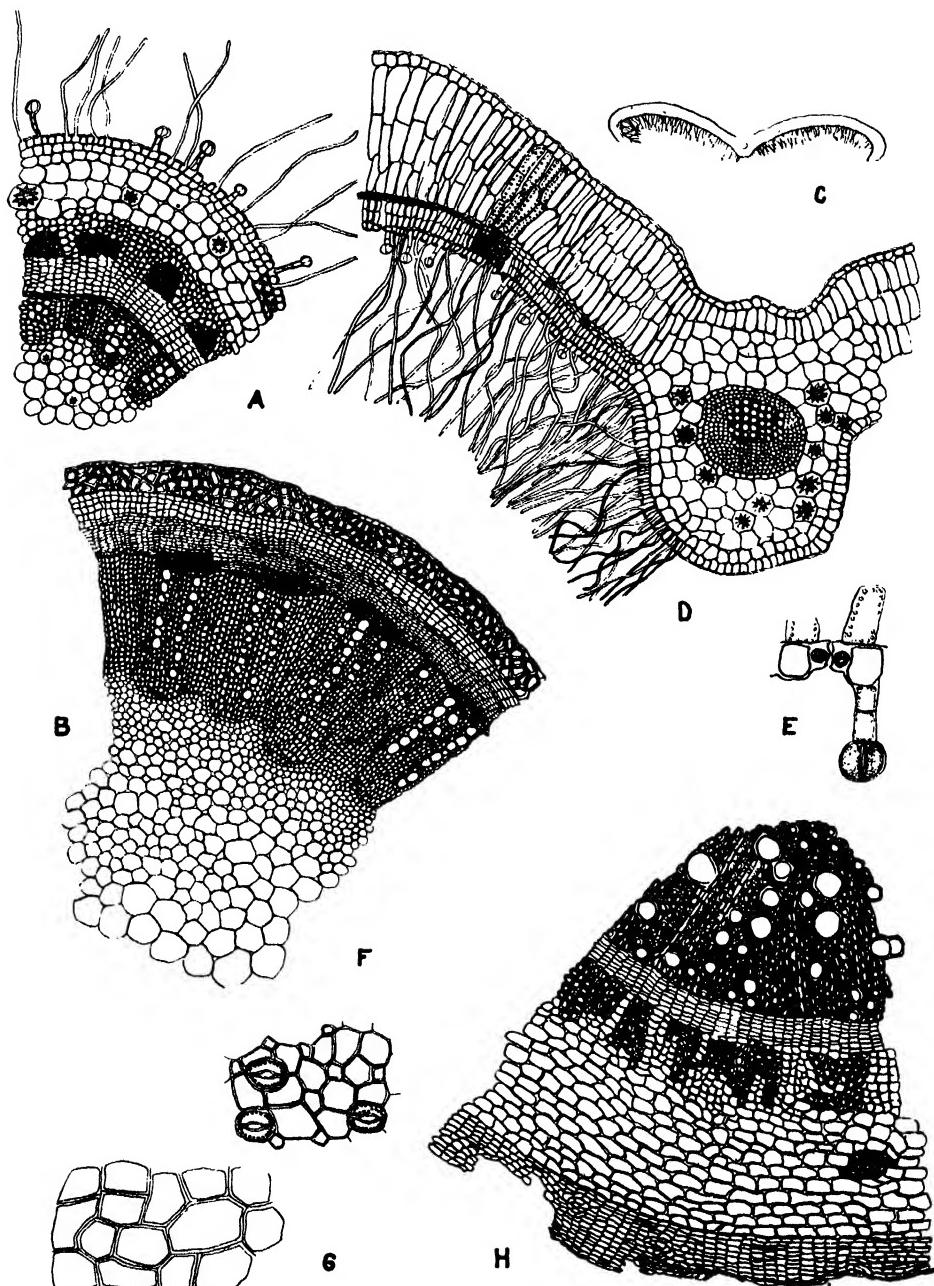
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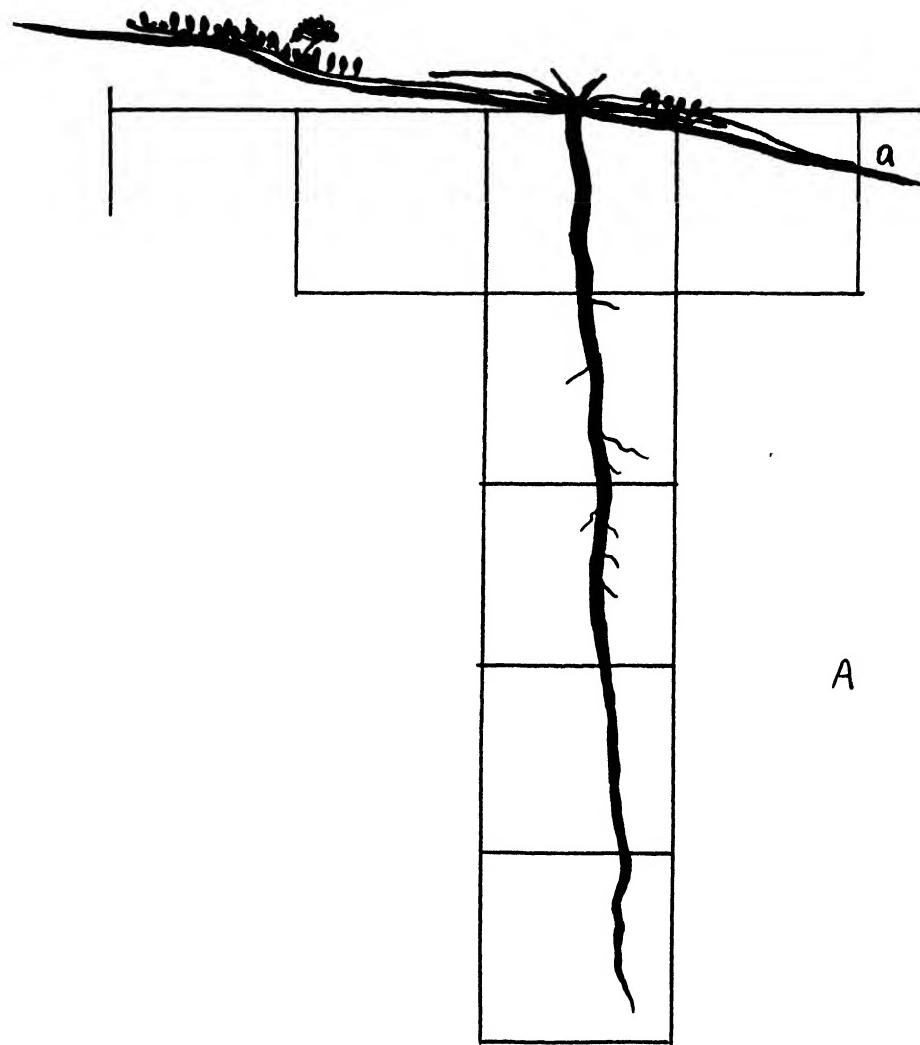
Plate 17. *Abronia umbellata* Lam.
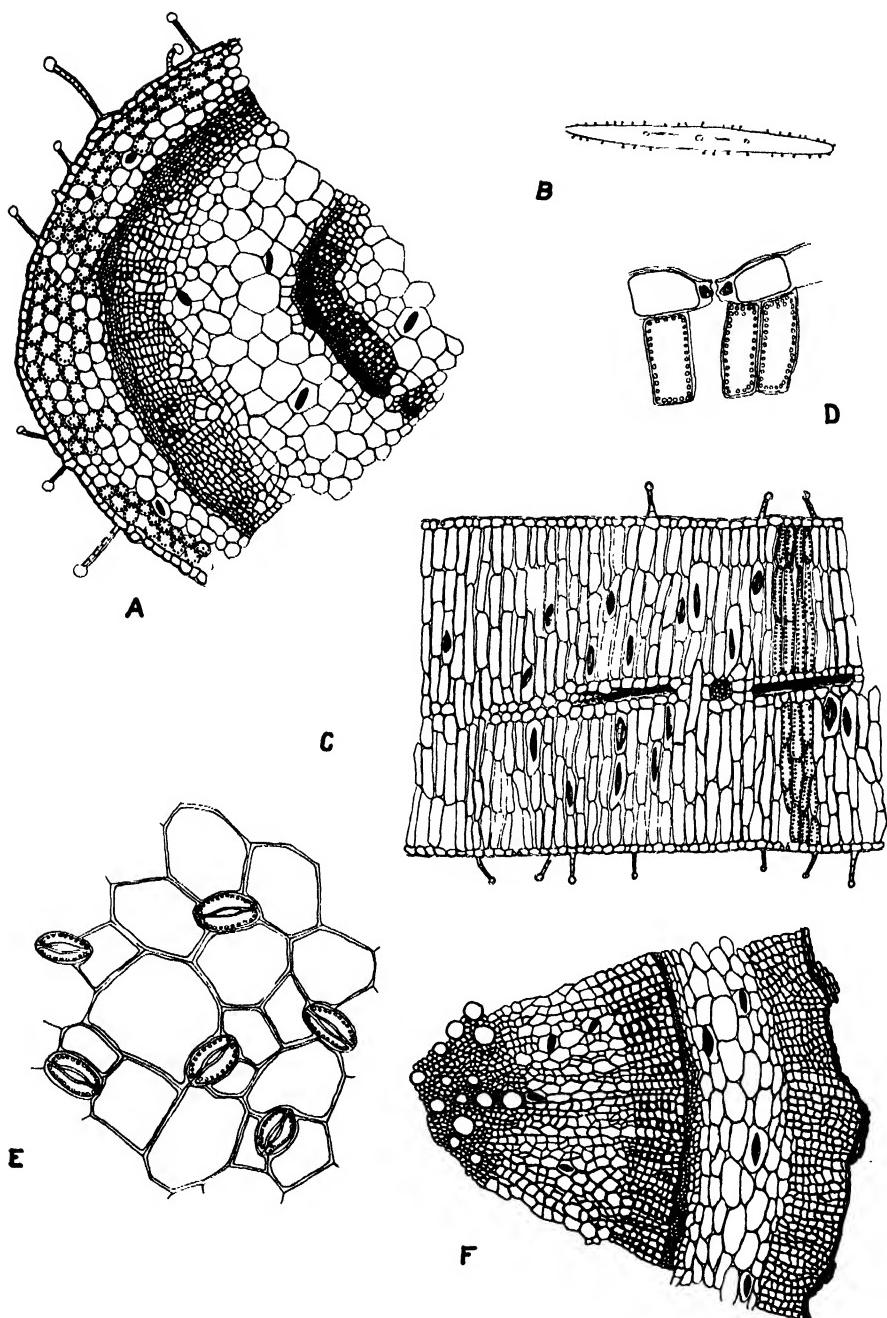
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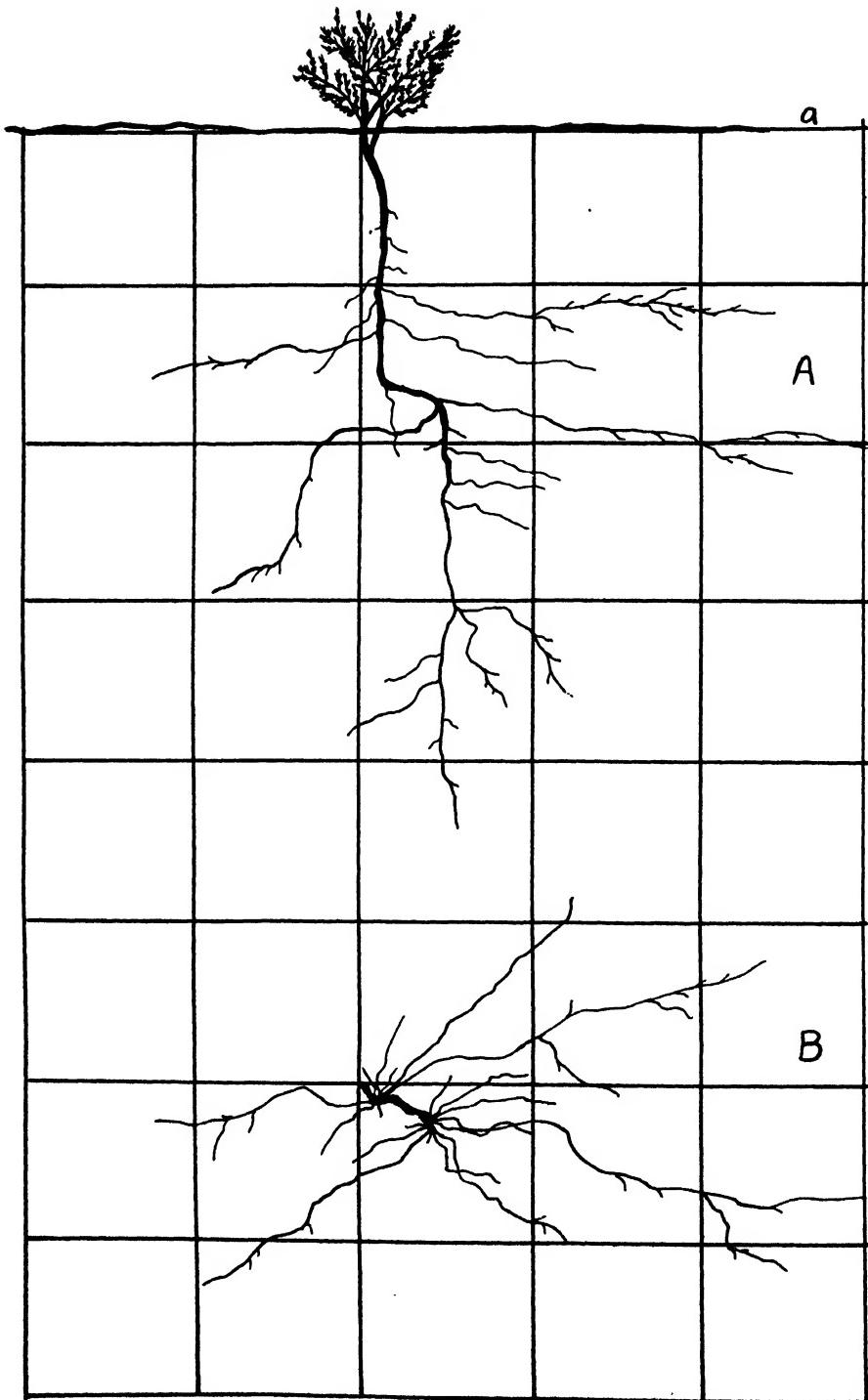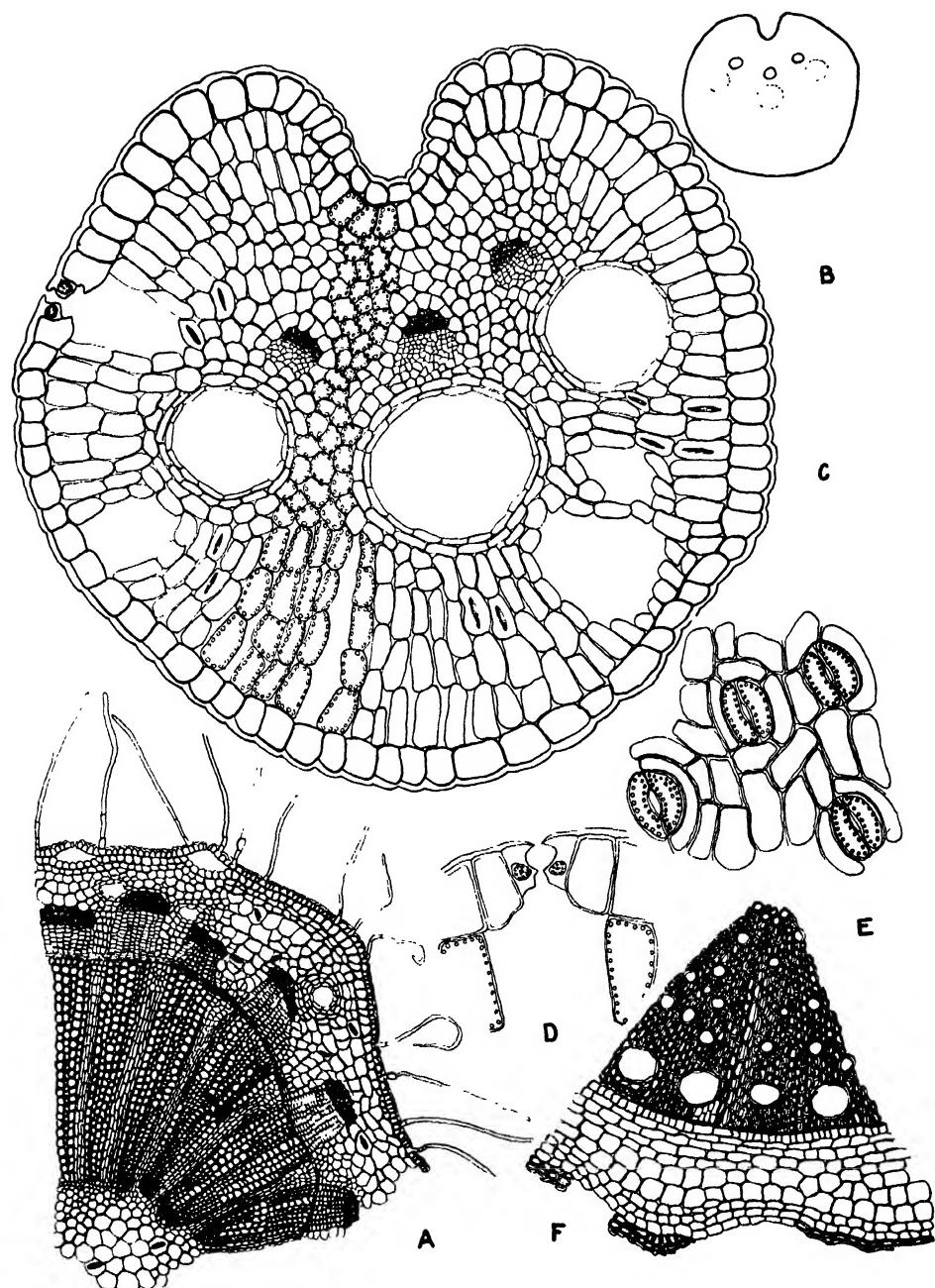
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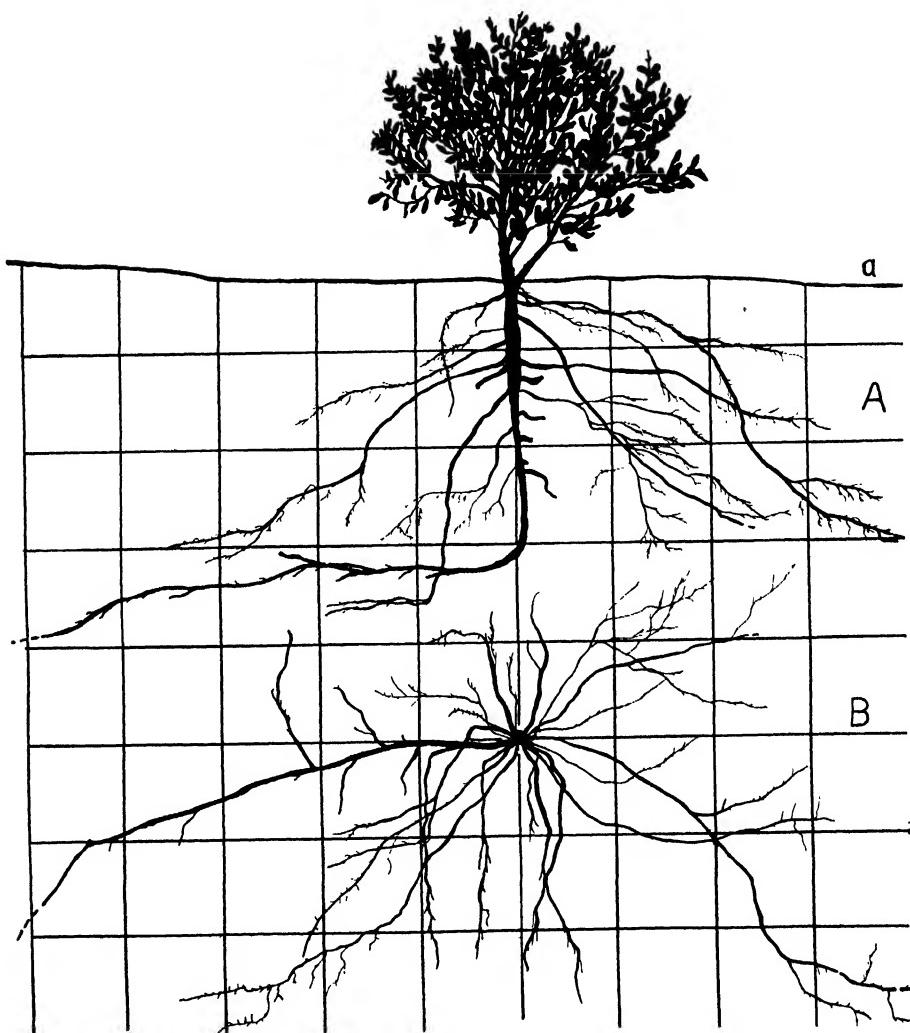
Plate 21. *Rhus integrifolia* B. & W.
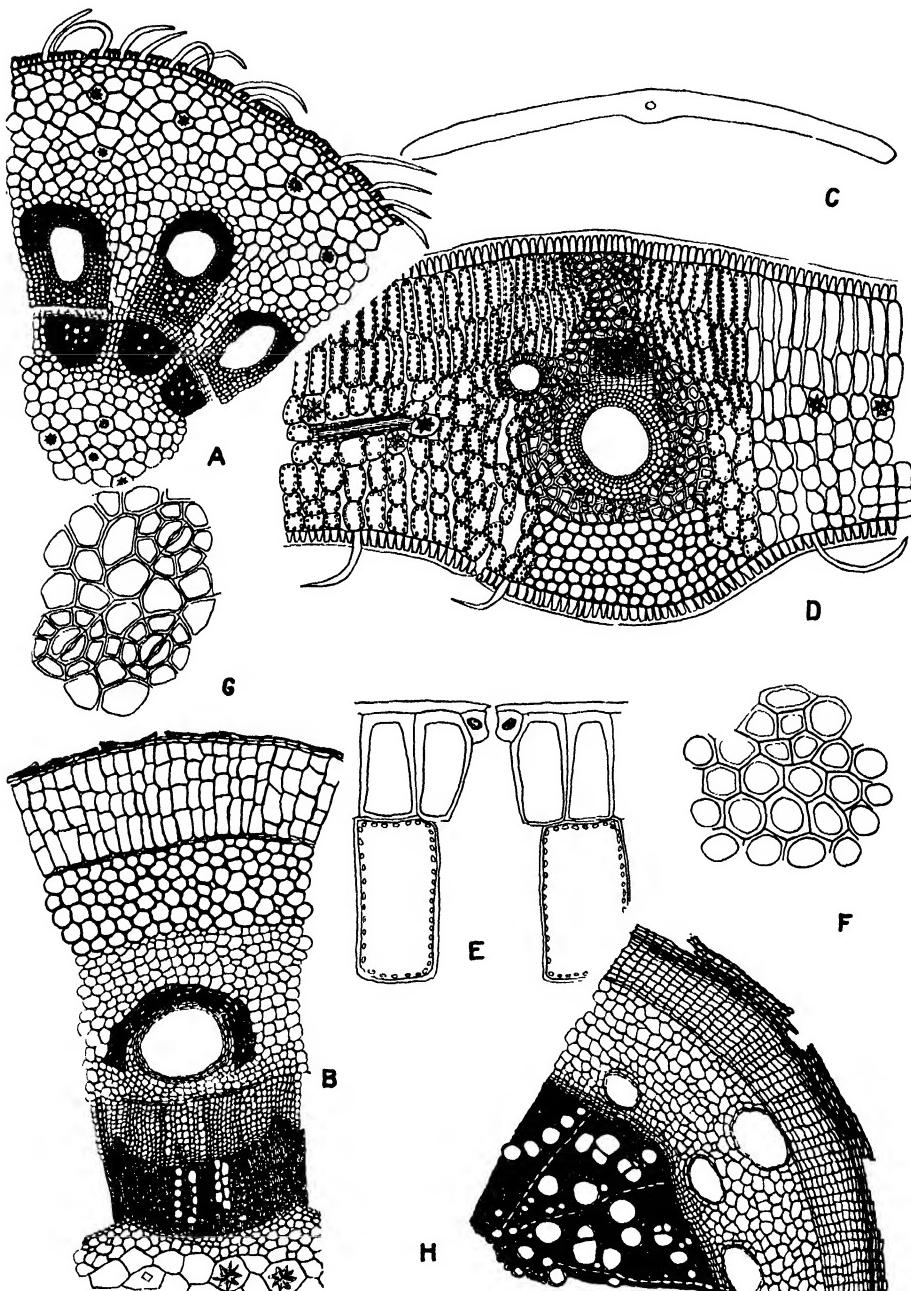
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FORESTS OF THE ILLINOIAN TILL PLAIN OF SOUTHWESTERN OHIO

By

E. Lucy Braun
University of Cincinnati

CONTENTS

FORESTS OF THE ILLINOIAN TILL PLAIN OF SOUTHWESTERN OHIO

I. INTRODUCTION

The Illinoian till plain in southwestern Ohio contrasts with adjacent areas in certain vegetational, topographic, and soil features. For this reason it may be considered as a distinct region. Vegetationally, it is a part of the eastern deciduous forest formation, but is delimited by differences in developmental stages and in forest composition from surrounding areas. Swamp forests in which pin oak, sweet gum, white elm, and red maple are important, prevail or did before man cleared and otherwise changed the environment. Common mesophytic trees of the adjacent Cincinnati region and of smaller maturely dissected areas in the general till plain region, as sugar maple, tulip, sweet buckeye, and basswood are absent or rare on the Illinoian till plain in Ohio.

The accompanying map (Fig. 1) shows the glacial boundaries, the area of till plains considered in this paper, and the location of the "Flats" in Indiana. No term has been used to designate this plain in Ohio, though various local names including "flats" are in common use.
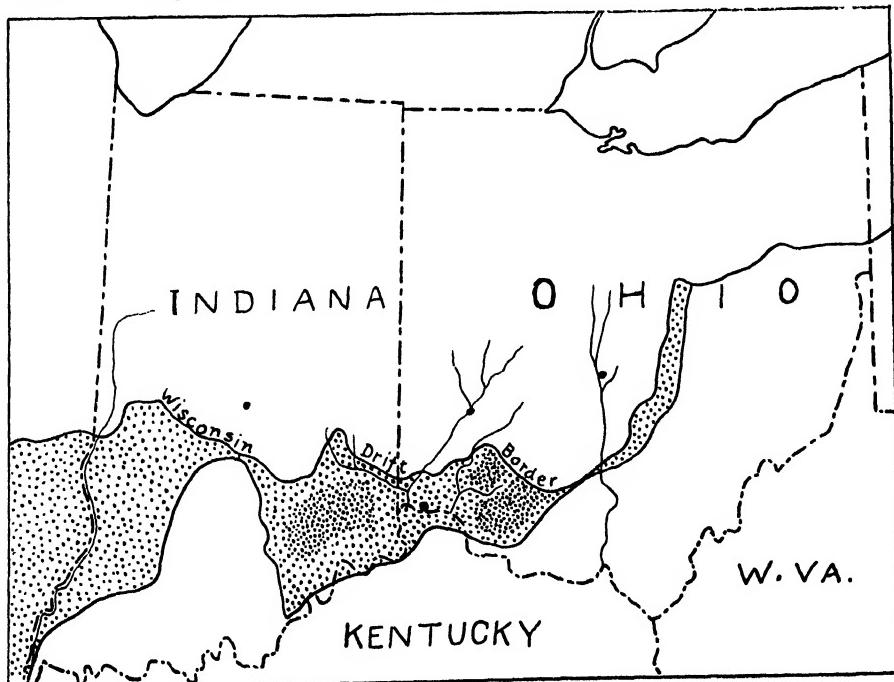
Fig. 1. Map of Ohio and Indiana showing Illinoian drift area (stippled) and boundary of Wisconsin drift. Location of "Flats" of Indiana and of undissected till plain of southwestern Ohio indicated by closer stippling. (After Leverett, 1902, 1915, and Deam, 1921.)

The great southward extending lobe of Illinoian glacial deposits in Ohio and Indiana is divisible into three parts: an eastern section, the Illinoian till plain under consideration in this paper; a central strongly dissected section lying for the most part between the Little Miami and Whitewater rivers (approximately the Cincinnati region); and a flat western section, the "Flats" of Indiana, very similar to the eastern section. Local communities on the occasional small flats in the central dissected section are ecologically a part of the vegetation of the till plains (Braun, 1916). In the "Flats" of southeastern Indiana are large areas of forest comparable to those of the Ohio till plain.

Elsewhere, swamp forests resembling these are local, occupying parts of the lake plains, marked depressions in the youngest glacial plain, or commonly, small stratum plains on impervious rock. The last are seen on the flats of Devonian shale in Kentucky and Indiana (Muscatatuck Flats), and on level parts of the Allegheny and Cumberland plateaus at the headwaters of streams. Such areas are relatively small in extent, and while they contain some of the species, and have much of the aspect of the swamp forests of the till plains, they nowhere display the complexity of communities or the successional development marking the vegetation of the till plain of southwestern Ohio.

The area under consideration covers approximately 1,500 square miles to the east of the Little Miami River; it is flat or nearly flat upland lying at an elevation of about 900 or 1,000 feet. Throughout its extent, bedrock is buried under a mantle of glacial drift of Illinoian age which varies in thickness from 10 to 50 feet (Fuller and Clapp, 1912). The valleys of the larger streams trench this plain to a depth of 100 to 300 feet; smaller streams except in the immediate vicinity of large ones, flow in shallow valleys few of which cut deeply enough to enter the bedrock. Although this area is far older than the glacial plains to the north which are of Wisconsin age, it, nevertheless, is still topographically young and many places remain as yet undissected by even the smallest streams. Initial inequalities in the drift deposit are indicated by the very shallow depressions only a few feet in depth which are still discernible in many places. These topographic features make for poor run-off and a water-logged soil.

II. HABITAT FACTORS

The habitat is essentially an undissected plain with fine-grained soils, water-logged, and hence poorly aerated. Man's modification of the area by ditching and clearing has made changes which are far-reaching and as a result the habitat of today is not the extreme habitat in which the vegetation developed. Soil water especially, and hence soil aeration and humus decomposition have been affected. Because this is a glacial topography for the most part unmodified by erosion, vegetational development apart from that brought about by climatic changes has in the main been directed by biotic factors.

However, the major vegetational features are due to topography and soil conditions. Bare areas do not exist; pioneer communities have long since been crowded out by later vegetation, and all habitats have been affected by the reaction of vegetation. Certain soil factors, whether antecedent to or resultant from present communities, are significant and are in need of further study.

Temperature and Precipitation

Temperature and precipitation data secured from U. S. Weather Bureau records of one station (near Batavia) on the till plain, and from stations adjacent to the till plain to east, west and north, show essential climatic uniformity throughout this and adjacent areas. Temperature ranges from a January mean of 30°F. to a July mean of 75°F., approximately, with a maximum annual temperature range of about 120°F. The frostless season is nearly 6½ months. Rainfall for the region is approximately 40 inches, fairly evenly distributed throughout the year. Due to the patchy precipitation resulting from summer thunderstorms and the tendency of such storms to follow definite courses, certain areas are less often visited by heavy rains and have the reputation of being "dry islands." These differences do not appear in the few available records. They may have some bearing on the distribution of the characteristic shrub species and be responsible in part for the absence of these shrubs from some large areas. In drought years, the effect is more disastrous in these places. In those areas of the flats in which beech and white oak suffered most from the 1930 drought the characteristic shrubs are most poorly represented, indicating that these areas have in the past suffered in the same manner.

Evaporation

Evaporation, usually considered to be of major importance in ecological work, is here considered to be of little value in explaining differences in adjacent communities. Uniformity of topography and hence initial similarity of evaporation throughout the area—except as affected by differences of rainfall—preclude the possibility of this having been an initial cause. Any differences which may exist now are the result of, not the cause of, differences of forest cover.

Light

Differences in light are due to the amount and kind of vegetation covering, not to any initial conditions. They become extremely important in the course of these biotic successions, perhaps determinative in the ecesis of certain species during successional development. Light as a factor in the germination of seed of sun plants may be important (Hutchings, 1932). Light, however, could scarcely have been a factor in bringing about differences in initial forest stages.

Soils

The soils of the Illinoian till plain are all fine-grained and classified as silt loams. Weathering has proceeded so deeply that few pebbles remain. While all have developed from originally calcareous drift, the soluble carbonates have been leached so deeply that the soils are acid. The earlier soil surveys (Coffey and Rice, 1915; Goodman, Allen and Phillips, 1917) recognized three types of upland soils in this area: the Cincinnati silt loam, the Rossmoyne silt loam, and the Clermont silt loam. Later surveys (Taylor et al, 1928; Conrey, mss. map) have distinguished additional types or subtypes.

The Cincinnati silt loam has attained approximately a mature state of development. It occurs on all of the hillier sections of the glacial plains, usually on the slopes bordering stream valleys. The Rossmoyne silt loam is intermediate in position between the Cincinnati silt loam and the Clermont silt loam. It occupies the very low and scarcely noticeable ridges which traverse some of the flattest areas and occurs as a narrow belt around the borders of the flats.

The Clermont silt loam is most important and gives to the area much of its distinctive character. It is ashy white when dry—hence the name "white clay" which is commonly applied. The subsoil is strongly mottled with brown iron stain. This is the soil which prevails throughout the flattest parts of the Illinoian till plain; throughout most of the area which may properly be designated as "plain." Locally, and usually in the indefinable depressions about the heads of streams, a darker soil has developed—the Blanchester silt loam. The Clermont and Blanchester silt loams have developed under conditions of poor drainage; the Cincinnati silt loam under good drainage; the Rossmoyne, intermediate, and demonstrates the soil changes which have taken place where the marginal part of the Clermont silt loam has been affected by developing drainage lines.

On cleared land, areas of the several soil types are readily distinguished by color. In forest land, the surface layer is slightly darkened by humus in all types, but differences are evident at depths of 4 or 5 inches.

The accompanying map (Fig. 2) shows the approximate extent and location of the Clermont (including Blanchester) silt loam; or, the area of the undissected till plain.

The combination of fine-grained soils with slight or no granulation, exceedingly compact a few inches beneath the surface, and level land undissected by streams results in very poor surface drainage. Water stands in fields and even in forests after heavy rains, and in seasons of normal rainfall, throughout much of the winter and spring months. This introduces a decided handicap to land utilization. Attempts to overcome these conditions and drain the land, thus making it more fit agriculturally, have been made and have resulted in profound changes in the environment. Fields are ditched or tile-

drained or both; ditches 1 to 3 feet deep extend alongside of every road; and "township ditches" collect the water from the field ditches and carry it some-times several miles to streams. Such township ditches may be 3 to 5 feet in depth, for some flow must be possible during heavy rains if they are to carry off surface water. The meandering, swampy and shallow creek valleys have in many places been straightened and deepened to serve as ditches. In fact it is now difficult to find any which do not flow in straight lines and turn at
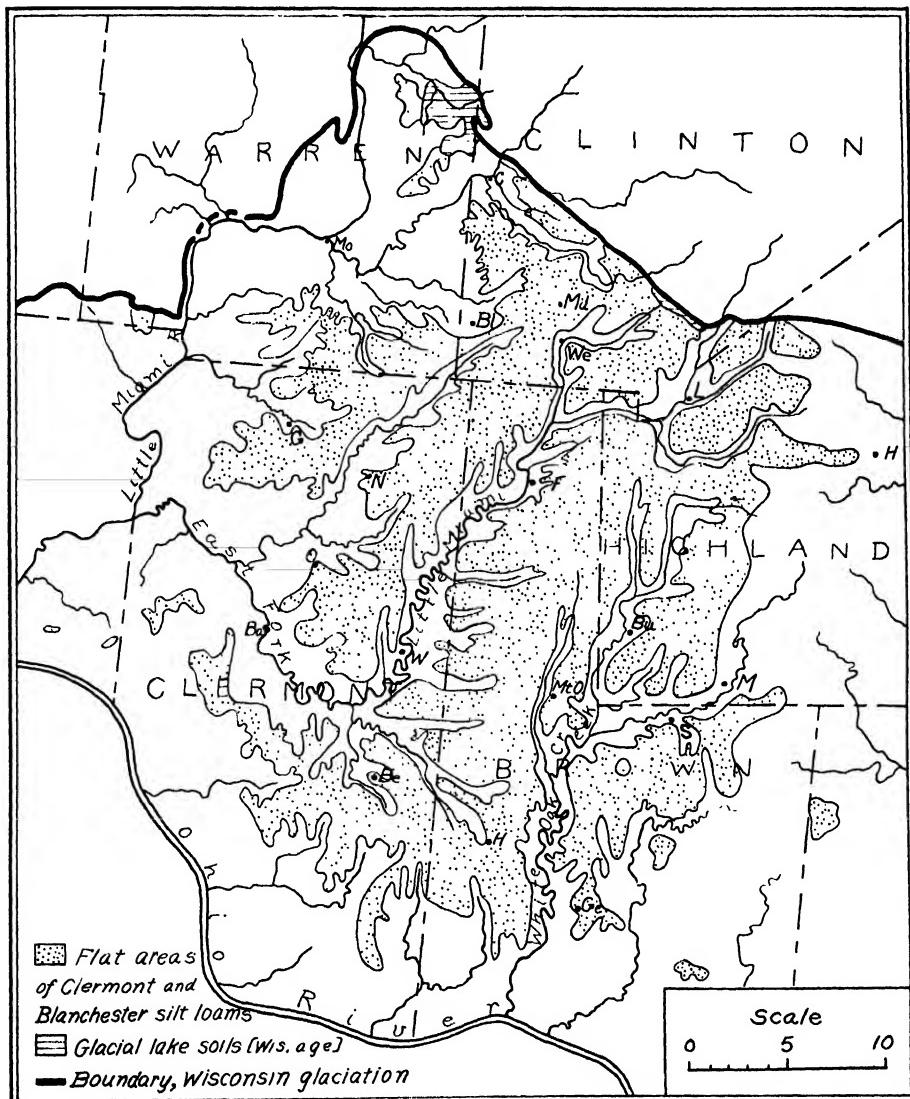
FIG. 2. Map showing extent and location of Clermont (including Blanchester) silt loam; or, the area of the undissected till plain. (After Coffey and Rice, 1915.)

right angles.　As these wet flats are within the Revolutionary Land Grant area of Ohio, settlements were made here over 125 years ago and the first clearings made at that time.　Most of the changes due to ditching are, however, relatively recent and followed the introduction of tile-drainage and the maintenance of the township ditches.　Fields which now grow corn successfully used to stand under water all winter and even all summer in wet years. Farmers tell of places—now fairly good corn fields—where it was necessary for miles to walk logs and jump from root to root in the forest swamp to keep out of the water, even in August.　Conditions of this sort no longer exist; the environment under which the existing forest types developed is not represented in the area today.　The environmental conditions which now exist —atmospheric humidity, the conditions of soil, soil water, even to some extent soil composition—are not the conditions under which the vegetation of the till plains developed.　The environment, unmodified by man, is gone, and the return of forests similar to the original is no longer possible.　Neither is the secondary vegetation now coming in like that which started as little as 25 years ago.　It is justifiable to assume that previous to disturbance the water table was higher and that ponds were more extensive and more permanent than now.

Soil Water

Measurements of the amount of soil water, unless carried on through enough years to cover entire cycles of weather including periods of extreme drought and of maximum rainfall mean little in an area where extremes of habitat are absent.　Also, soil water if measured now, would not indicate the conditions under which any except the youngest secondary communities developed.

Soil Aeration

Aeration is dependent on soil porosity and the level of ground water, which fluctuates with climatic cycles.　In average years the water table is at or near the surface in broad flats and above the surface in depressions from about November to May or June.　In dry years it is at or close to the surface in depressions; in drought years, many depressions are dry.

Soil Temperature

Due to the high water content, especially in spring, soil temperature is lower than in hillier areas.　This results in a retardation of growth in spring which is particularly evident in time of leafing of trees and blooming of shrubs. This difference on the wet flats and on adjacent hilly land may amount to one or two weeks in the same species.

Nitrogen Content and Humus Content

The Clermont silt loam and the Blanchester silt loam, which differ in organic content—the Clermont silt loam "is particularly deficient in organic

matter" (Taylor et al, 1928)—support partly unlike communities. Chapman (1933), experimenting with the effects of nitrogen on the growth of seedlings of tulip tree, selected Clermont silt loam as a medium for growth because of its small content of organic matter. This work indicates that the scarcity on the till plain of tulip, which is not a nitrate accumulating species, may be accounted for by the absence of nitrogen from the soil. The absence of other common mesophytic forest trees from areas of Clermont silt loam may be due in part at least to this factor.

Hydrogen Ion

Hydrogen ion is here a factor of importance only in so far as it exerts a selective influence on certain acid soil species, and in its probable relation to soil organisms and consequent decomposition processes. All of the soils of the till plains are acid, ranging from pH 6.5 to pH 3.5.[1] The range of pH values in the several successional stages and beech subclimax forest is shown in Table 1. From this it will be seen that the soils of initial forest stages are

TABLE 1. Range of pH values of soils at one and five inch depths in the several successional stages and beech subclimax.

pH values	Initial		Intermediate		Late		Climax	
	1 in.	5 in.	1 in.	5 in.	1 in.	5 in.	1 in.	5 in.
3.5 — 3.9........	2	..	2	1	2	..	..	..
4.0 — 4.4........	10	13	4	7	3	3	1	1
4.5 — 4.9........	23	27	5	14	5	9	3	5
5.0 — 5.4........	10	1	13	5	2	2	2	3
5.5 — 5.9........	..	1	5	1	1	..	6	1
6.0 — 6.4........	..	..	1	..	2	1	3	..
Number of samples tested.	45	42	30	28	15	15	15	10

somewhat more acid than those of intermediate and late stages, and the range of reactions less than in later stages. There is a slight widening of the range of reactions in later stages, together with a tendency to less acid soils—conditions agreeing with the observations of Geisler (1926).

The yellow Rossmoyne silt loam soils mostly range between pH 5.0 and pH 6 0. The white Clermont silt loam and the darker Blanchester silt loams are generally more acid. pH 4.0 to 5.0. Soils of secondary meadows on the Rossmoyne silt loam have pH values between 5.0 and 5.5; those on Clermont silt loam and Blanchester silt loam, though floristically very distinct, are similar in soil acidity, with pH values between 4 and 5, mostly around 4.5.

The most acid soils are those under Sphagnum and Polytrichum hummocks, and in clumps of Vaccinium. Soils from Sphagnum mounds range

[1] pH values were determined electrically for 312 soil samples, using quinhydrone electrodes. For these determinations, the writer is indebted to Miss Emily R. Hess.

from pH 3.6 to 4.2; from Polytrichum mounds, pH 3.5 to 4.2; from among
Vaccinium bushes, pH 3.8 to 4.8.

A few of the plants sometimes found in forest communities, as *Mitchella
repens*,[2] *Chimaphila maculata, Vaccinium vacillans* and *V. stamineum,* are
generally recognized as acid soil species, rather than swamp species. A few
commonly require acid soil and abundant moisture; among these are *Sphagnum subsecundum* Nees, which is locally abundant, *Aspidium noveboracense,
Spiraea tomentosa* and *S. alba, Pyrus melanocarpa, Viola lanceolata.*

There is little relation between pH and topography, except where dissection
is sufficient to introduce drained slopes (see transect, Fig. 34). pH values
for soils in areas of transects are shown along the profiles accompanying
transects (Figs. 28, 30, 32, 34). No significant differences could be observed
between pH values of the earlier stages of the PO → WO → B and RM → B
successions.

Root Competition

Observations on the root systems of a number of plants indicate that
adaptability of root system and root competition in the upper soil layers are
important factors in determining the ability of plants to occupy these areas.
The conditions of soil water and soil aeration are unfavorable to deep root
penetration.

The adaptability of beech, permitting it to develop a very shallow root
system in the wettest and most poorly aerated soils, may account in part for
the early entrance of this mesophyte in succession. It also results, in times
of severe drought, in the dying out of this species in depressions, thus opening
up small areas for re-invasion by trees.

The development of shallow root systems by beech, white elm, red maple
and occasionally sweet gum increases root competition in all areas where
these trees are present, and may be a factor in accounting for the paucity of
ground vegetation in those communities in which these trees are important.
Under beech trees in the wettest places—where the mat of fine fibrous roots
fills the upper 3 to 5 inches of soil—only such superficial plants as *Mitchella
repens* can grow. On the other hand, the greater abundance of shrubs and
herbs in many pin oak and white oak areas (neither of which trees develop
shallow root systems) may be due in part to the lesser competition in these
communities. Peculiarities of the root systems of some of the plants of the
till plain have been considered in a separate paper (Braun, 1936).

Topographic Factors

Topographically, the habitat is a plain, almost level, which here and there
contains depressions a few inches or a few feet in depth, or ridges of like
proportions. These minor inequalities in the land surface result in differences

[2] Nomenclature in this paper according to Gray's New Manual of Botany, 7th Ed., 1908, except as
noted.

in the soil water factor which are reflected in the distribution and grouping of tree species in the forest. The sequence of communities in and around depressions and the sequence from ravines to flats are definitely related to topography. This is demonstrated by a series of transects, Figures 28, 30, 32, 34.

III. PRIMARY VEGETATION

The original forest of the undissected till plain was a mixed forest composed of about 15 tree species segregated into more or less distinct communities in different stages of successional development. In the forest as a whole, beech, white oak, pin oak, red maple, white elm, shellbark hickory and sweet gum are, in the order named, the most important species. Of this original forest, only isolated remnants remain, few of which are as large as 100 acres. Because of this, the relation of communities to habitat, the inter-relations of communities and successional development are often obscured.

All of the forest communities, of which there are about 25 distinguishable, belong to hydrarch successions in which three developmental stages are recognizable: (1) Initial forest stages; (2) Intermediate stages; and (3) Late stages. The initial forest stages are not pioneer—the pioneer vegetation of these wet uplands entered many thousand years ago with the first invasion of plants into the new glacial deposits; the late stages may be thought of as resulting in a physiographic climax, to persist as long as the till plain remains undissected and undrained. Drainage permits the entrance of other mesophytic species and in time results—if stream cutting does not go too far—in the development of the mixed mesophytic forest, the climatic climax of this geographic area.

Initial forest stages include several segregates of what may be termed the pin oak-red maple-elm-sweet gum associes. They occupy depressions, many of which are not deep enough for the surface of the ground to appear damp in summer, though it may at times be covered with shallow water. Depressions are usually small, a few hundred feet across, and seldom do all of the species occur in any one depression.

Intermediate stages are marked by the appearance and increasing importance of species which later become dominant or codominant, namely, shellbark hickory, white oak, and beech; and by the disappearance, first of pin oak, later of white elm, sweet gum, and red maple.

The white oak-beech associes and certain phases of the beech forest are late stages; the beech association may be considered the climax of the undissected areas, i.e., a physiographic climax. The rims of depressions, the low ridges, and the margins of the plain indented by the shallowest ravines support beech or white oak or a mixture of these two species, together with an admixture of other more or less mesophytic species. All intermediate locations,

and some of the depressions and some of the ridges, if broad, support the intermediate forest stages.

Dissection changes the water relations, and initiates new conditions which cause the disappearance of all hydro-mesophytic species and permit the entrance of mesophytic species. The forest of areas where dissection is beginning approaches the regional climax type—the mixed mesophytic forest of southwestern Ohio and adjacent areas.

Vegetational development on the till plain is shown by the diagram (Fig. 3) of primary successions. All combinations of the constituent species of each stage are possible and lead to considerable complexity and overlapping of communities. The accompanying chart (Fig. 4) shows tree occurrence and importance in developmental stages of the till plain forest and in the physiographic and regional climaxes, based upon counts in primary areas.

In Table 2 are listed all of the trees, in the order of the presence percentage[3] of the species. Presence percentage (Pr %) is determined from occurrence in 50 forest areas of the till plain for which composition lists were made. The low presence percentage of sweet gum—considered one of the important trees of the swamp forest—is due to its almost complete limitation, geographically, to the southern half of the area. The percentage of each species in the forest of the till plain as a whole, based upon a count of 3,707 trees, is also given. Additional columns in the table give the forest canopy composition of nineteen representative areas of primary forest in the flats,
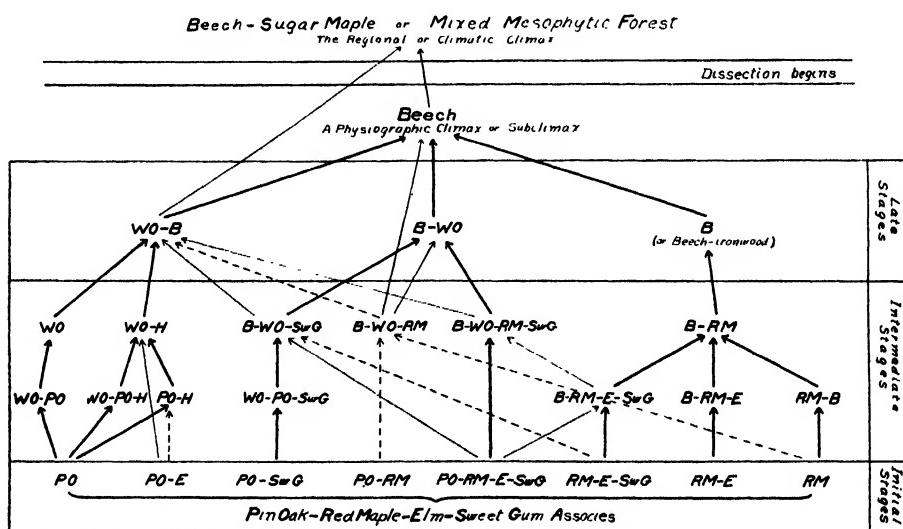
FIG. 3. Diagram of primary successions on the till plain.

[3] By presence is meant the more or less persistent occurrence of a species in all the stands of a certain community." Braun-Blanquet (1932). As defined by Cain (1932) "Presence concerns the degree of regularity with which species reoccur in different examples of an association." This may be expressed in percentage (as in Table 2) or, less exactly, in the 1 to 5 scale suggested by both Braun-Blanquet and Cain.

FIG. 4. Chart of tree occurrence and importance in developmental stages of the till plain forest and in the physiographic and regional climaxes, based upon counts in primary areas.

TABLE 2. Percentage Composition of Trees of Forest Canopy in Representative Areas of Developmental and Climax Stages of Succession on the Till Plain and of the Regional Climax.

	AREA AS A WHOLE		INITIAL STAGES		INTERMEDIATE STAGES			LATE STAGES	PHYSIOGRAPHIC CLIMAX OR SUBCLIMAX	REGIONAL OR CLIMATIC CLIMAX
		Pr. %	PO	PO-RM-E-SwG & RM-E-SwG	WO-PO-SwG, WO-PO & WO	B-RM-E-SwG & B-RM-E	B-WO-RM & B-WO-SwG	WO-B	B	Mixed Mesophytic
Number of trees	3707		208 · 172 · 400	77 · 82 · 150	32 · 63 · 120 · 295	249 · 70 · 60 · 379	148 · 120 · 187 · 674	349 · 210 · 191 · 357 · 1309	213 · 171 · 384	75 · 126 · 405
Forest area, number			1 · 2	3 · 4	5 · 6 · 7	8 · 9 · 10	11 · 12 · 13	14 · 15 · 16 · 17	18 · 19	20 · 21
Fagus grandifolia, beech	86	36.2	1.4 · 1.6 · 1.2	14.6*·14.6*·14.2	31.2·65.1·78.5·2.0	37.7·51.4·76.1·46.6	49.7·50.8·43.6	21.5·31.4·37.2·39.5·34.6	80.3·88.3·83.8	62.6·47.0·42.4
Quercus alba, white oak	80	23.0	8.2·19.2·12.5	1.3 · 2.4 · 1.6	9.0·9.5·6.6·10.0	4.1·0.0·1.0·29.0	26.0·23.0·20.5	39.5·30.0·31.5·33.3·34.4	1.4·2.3·.8	.8·2.0
Carya ovata, shell-bark hickory	80	4.9	8.2·4.0·6.2		7.4·6.6	2.4·1.0	5.4·1.0·2.0	13.7·9.0·1.6·4.5·6.8	4.2·2.3·3.4	.8 · .7
Quercus palustris, pin oak	74	11.1	71.2·63.4·67.5	16.8·37.7	8.4·12.7	4.8	3.2·6.1·7.5·1.0	6.3·6.2·4.7·2.5·4.2		
Acer rubrum, red maple	72	7.3	.5 · .7	9.1·46.3	3.0 · .7	.7·4.8·14.3·8.3	18.2·3.3·7.0·8.4	1.2·7.1·8.9·12.0·6.7	4.7·1.2·3.1	6.3·5.0
Nyssa sylvatica, sour gum	66	2.8	.5·5.8·2.7	9.1 · 4.8	3.1	1.0	5.2	1.2·3.1·1.0·2.0·1.8	.5·1.2·.8	.8·1.2
Ulmus americana, white elm	58	5.0	5.3·1.0·4.0	14.3·17.1		11.2·4.3·11.0·9.5	1.0 · 1.6	2.0·3.1·7.8·3.1·3.0	7.5·7.0·7.3	.5
Quercus bicolor, swamp white oak	50	1.1	3.3·3.2·2.7	5.2	12.5·6.4	3.0·1.2·1.4	9.5 · .5	1.6		
Liquidambar styraciflua, sweet gum	46	3.5	.5	9.1·13.4	15.6	2.4·12.4·17.1	11.3			
Quercus velutina, black oak	40	1.8	1.4·3.2·1.7		3.0·3.2·6.6·4.4	4.1	4.7 · .5	8.9·2.0·1.6 · 3.1		.3
Quercus imbricaria, shingle oak	40	.2			.7		2.0	.3		
Carya alba, white-heart hickory	28	.7			3.2 · .7	.8		1.0 · 1.6		
Fraxinus americana, white ash	26	.2		1.2		.4·1.4	.3	2.5·4.7 · .5		2.6·6.3·5.0
Acer saccharum, sugar maple	20	.4						3.2·2.0 · .5		8.0·15.0·14.8
Liriodendron tulipifera, tulip tree	10	.2						.6·2.1		17.3·13.5·12.0
Quercus rubra, red oak	8	.1			2.0	1.3		.2	1.4	4.0·4.0·1.2
Carya microcarpa, small-fruited hickory	8	.1						.1		
Carya cordiformis, bitternut hickory	6	.1					.5	.1		
Fraxinus pennsylvanica, red ash	6					1.6		.1	1.3 · .8 · 1.2	1.3 · .8 · 1.2
Fraxinus profunda, pumpkin ash	4					3				
Sassafras variifolium, sassafras	2									
Tilia americana, basswood	2									1.3·4.0·9.1
Juglans nigra, walnut										1.3·3.5·3.2
Ulmus fulva, red elm										1.3·2.0
Prunus serotina, wild black cherry										1.3·1.7
Celtis occidentalis, hackberry										1.3 · .8 · .7
Quercus Muhlenbergii, chestnut oak										.7
Carya glabra, pignut										.5
Aesculus octandra, sweet buckeye										.3
Juglans cinerea, butternut									.8	.3

and for comparison, of two areas of mixed mesophytic forest—the regional or climatic climax. These are grouped in successional stages, and demonstrate something of the variations in composition and in importance of constituent species possible in the several stages. For each segregate or group of segregates of the associes of the several stages the percentages are listed; these are based on the counts given for the selected areas and a few additional counts. In all cases the number of trees from which the calculations were made is given. The occurrence, in forest communities referred in this table to "initial stages" of trees more characteristic of later stages, is due to humps and land surface inequalities which offer a fairly suitable environment to trees normally occurring later. Similarly, the occurrence in "late stages" of trees of the initial stages is due either to the occurrence of scattered very small depressions in which one or several pioneer trees persist (the group really not a part of the later successional stage by which it is surrounded) or to windfalls which have resulted in lighter places more suitable to pioneer species. These features of distribution are amply demonstrated in transects charted in a number of representative forest areas (see Figures 28, 30, 32, 34).

Shrubs are abundant in the forests of the till plains, and constitute a floristically important element of the vegetation. Thirty-five species including six woody climbers are recorded—several times the number which occur in any one successional series in the edaphically-diversified adjacent Cincinnati region. The most characteristic of the shrub species are: *Ilex verticillata* (4+), *Viburnum pubescens* var. *indianense* Rehder (4+), *Vitis labrusca* (4), *Spiraea tomentosa* (3+), and *Pyrus melanocarpa* (2-3). These are fairly generally distributed in the area (Braun, 1935a) ; presence is indicated by the numerals in parenthesis (following the 1-5 scale). Certain other rarer species are peculiar to the till plains, *i.e.*, do not occur in the regions to either side; these are *Spiraea alba, S. latifolia,*[4] *Rubus hispidus,* and *Viburnum Lentago.* Two species of Vaccinium *(V. stamineum* and *V. vacillans)* occur rarely; both are abundant in the Allegheny Plateau but local west of that section. A number of other shrubs, though not peculiar to the Illinoian plain, are abundant; among these are: *Cephalanthus occidentalis, Salix discolor, Rosa carolina (R. palustris), Rosa setigera, Viburnum prunifolium, Corylus americana, Cornus racemosa*[5] *(C. candidissima), Cornus obliqua,*[5] *Hypericum prolificum, Smilax Bona-nox.* For each of these the index of presence is 3 (except *Rosa carolina,* 4), lower than for most of the more characteristic species, though when present these species often occur in larger patches than do any of the others except *Spiraea tomentosa.*

The community relations of most of these shrubs are obscure, for they are most common at the edges of forests and in clearings or secondary meadows. All, however, occur in initial or intermediate stages of the primary

[4] Specimen referred by E. J. Alexander of the New York Botanical Garden to *Spiraea latifolia.*
[5] Fide E. J. Palmer, Arnold Arboretum.

forest, but do not flower or fruit as freely in the forest as in more open situations. In later successional stages, occasionally also in intermediate stages, a few common mesophytes appear, especially *Benzoin aestivale, Sambucus canadensis* and *Asimina triloba.* In any stage of the forest succession, poison ivy *(Rhus Toxicodendron)* may be present and so abundant as to dominate the ground layer. *Viburnum prunifolium* is peculiar in its ecological distribution, occurring occasionally in initial and commonly in intermediate stages in these hydrarch successions, and abundantly as a pioneer in xerarch successions of river and ravine slopes of the same geographic area.

The number of species of herbaceous plants in the primary communities is fewer than in surrounding dissected areas. Nowhere except in the openings is the ground at any time clothed with an herbaceous layer. The forest is remarkably poor in herbaceous plants. Very few of the plants of the mesophytic or xero-mesophytic forests of slopes are here, and few swamp species endure the dense shade. The usual display of vernal flora of deciduous forests is absent, though a few species—*Cardamine bulbosa, Ranunculus hispidus* var. *falsus* Fernald, *Polemonium reptans, Claytonia virginica* and sometimes *Anemone quinquefolia, Arisaema triphyllum,* and *A. Dracontium*—are scattered in the swamp forest. In the later successional stages, a few additional plants of the spring flora enter, especially *Podophyllum peltatum.* A number of more or less distinctive plants, absent or rare in adjacent areas, are found; some of these are mentioned here. *Mitchella repens* is abundant in mossy hummocks about tree roots and on the ground in later forest stages; *Chimaphila maculata, Medeola virginica, Uvularia perfoliata, U. sessilifolia,* and *Tipularia discolor* occur in intermediate or late forest stages. Among the plants of openings in the pin oak forest are *Phlox maculata* var. *odorata* (Sweet) Wherry, *Aureolaria (Dasystoma) flava* var. *macrantha,*[6] *Habenaria peramoena, Lobelia cardinalis, Viola cucullata, Aster umbellatus, Lilium canadense,* and *Gentiana Saponaria. Rhexia virginica, Viola lanceolata, Houstonia coerulea, Coreopsis, tripteris,* and some of the plants of the pin oak openings are more or less characteristic of meadow communities. Ferns are represented by *Onoclea sensibilis, Asplenium angustum* (Willd.) Presl. and *Aspidium Thelypteris* (all locally forming large patches); *Osmunda regalis* (in both meadow and forest communities); *Botrychium obliquum* (always scattered but generally present); and *Botrychium dissectum.*

Mosses are abundant and very prominent in early successional stages, becoming less so in intermediate stages, except on beech roots in very wet forests. Most important are species of Polytrichum, Catharinea, Mnium, Dicranum, Leucobryum, Thuidium, Climacium and Sphagnum. Of these, *Climacium Kindbergii* (R. & C.) Grout and *Sphagnum subsecundum* Nees are characteristic of the more open and wettest places.

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[6] Determined by F. W. Pennell, Academy of Natural Sciences, Philadelphia.

The forest of the till plain is, then, a mixture of hydro-mesophytic tree species, with which are associated certain shrub and herb species, which because of their community and geographic limitations, are peculiarly characteristic of the area under consideration. More detailed features will be treated with the discussion of the various forest stages and successions.

A. INITIAL FOREST STAGES

1. DEPRESSIONS

Developmentally, the *pin oak-red maple-elm-sweet gum associes* is the youngest forest stage of these glacial plains. It is rarely represented as an associes with four dominants, but more often as segregates[7] in which one to three of the above species dominate, and in which swamp white oak and sour gum may be present as secondary species.

Area 3 (Table 2) gives percentages of one area in which the four important trees of this initial forest associes occur together. This area is a depression from 3 to 4 feet lower than the surrounding area of beech-white oak-sweet gum forest (no. 12 of Table 2). It is a rather dense stand, though in the central (and lowest) part of the depression the trees stand farther apart, and young pin oak, red maple and sweet gum are entering. Except in the lowest part, this depression forest is somewhat past the pioneer forest condition and the admixture of beech marks the transition to the beech-white oak-sweet gum associes of the surrounding plain.

The most prevalent of the initial forest stages is the pin oak consocies, which is so much more important over most of the area than any other that it may be thought of as the most characteristic forest of depressions.

Pin Oak Consocies

The pin oak forest or pin oak opening at its best is an almost pure stand of pin oak in rather open or park-like formation, with a sedge ground layer (Fig. 5). In spring the entire sedge area may be covered with shallow water. The pin oaks usually range in size from 7 to 9 feet in circumference, b.h., occasionally reaching 11 or 11½ feet. Similar areas of younger trees, 4 to 5 feet in circumference, are sometimes seen. Some of these are primary, some secondary; this may usually be determined by position and successional contacts. Swamp white oak, sour gum, white elm, sweet gum, or occasionally white oak, may be present. Swamp white oak in these depressions may be 9 to 10½ feet in circumference. Most often, this forest contains very few small trees. The ground cover is dominantly sedge—*Scirpus atrovirens, Carex typhina, C. squarrosa, C. lupulina, C. Asa-Grayi, C. intumescens, C. crinita,*

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[7] Segregation and regrouping of the dominants of complex communities give rise to a variety of communities with different dominants. Segregates of the associes, as in the above instance, are associes-segregates. The term, associes-segregate, includes consocies, facies, and locies. The association-segregate is a climax unit (see Braun, 1935).

Fig. 5. Pin oak opening with sedge ground cover. Scattered small pin oaks point to future closing in of forest. May.

C. grisea, C. gracillima, C. caroliniana, C. tribuloides, and *C. stipata* [8] In spring, *Cardamine bulbosa, Polemonium reptans,* and *Ranunculus hispidus* var. *falsus* Fernald are conspicuous. *Phlox maculata* var. *odorata,* blooming in early June, is locally abundant (Fig. 6). *Lobelia cardinalis* is commonly present, and often *Chelone glabra* and *Habenaria peramoena. Aster umbellatus, Eupa'orium macula'um, Solidago rugosa,* and *S. canadensis* are of frequent occurrence. *Ilex verticillata* and *Rosa setigera* are usually present.

Successively older pin oak areas have a scattered stand of small pin oak and shellbark hickory as an understory. Their entrance does not at first change the aspect of the open forest; later, with decrease in light, the sedge ground cover becomes thinner and patchy. In places a very dense layer of small pin oak is seen, completely filling the space between the widely-spaced

[8] Species of Carex determined by K. K. Mackenzie.

older trees, and eliminating all intolerant herb and shrub species of the openings (Fig. 7). Such mass growth of young trees seems to be correlated with the sudden lowering of the water table by ditching: the sedge pond is changed to a wet flat; soil aeration is improved; the light conditions are still favorable for intolerant species, and pin oak enters in great density. Such areas are usually devoid of undergrowth though poison ivy may be present. The ground is covered by a mat of soggy oak leaves; standing water is clear but brown.

The gradual lessening of light with increasing numbers of trees more and more limits the area suitable to meadow herbs and shrubs. Thus these become limited to very small areas. The rarer species, seen only occasionally though sometimes abundant or dominating in the opening in which found, may have thus been circumscribed. Two such species are *Baptisia leucantha* and *Aureolaria flava* var. *macrantha,* each seen in but one opening.

It would seem probable that the shrubs and herbs previously mentioned as peculiar to the flats but most abundant along forest borders and in secondary meadows originally belonged to openings and pin oak openings, but have now been obliterated there with the closing in of the forest, a process locally hastened by the artificial drainage in the area. In one opening,[9] twelve of the shrubby plants previously listed occur; these include the five most characteristic shrubs *(Ilex verticillata, Viburnum pubescens* var. *indianense, Vitis labrusca, Spiraea tomentosa, Pyrus melanocarpa)* and one *(Spiraea latifolia)* found only here. Eleven of the more characteristic herbaceous plants in addition to sedges and grasses are here also. The trees of the opening are

FIG. 6. *Phlox maculata* var. *odorata* in pin oak opening. June.

[9] Northwest of Blanchester, in Warren County.

relatively small—averaging about 4 feet in circumference—but the aspect is characteristic of the typical pin oak opening. The location of this opening, at the end of a rather elongate but irregular second growth stand of pin oak might cast some doubt upon its primary nature. However, the trees here are larger, older, and more unevenly aged than in the adjoining secondary forest, but not old enough to have been cut for timber at the time the adjacent forest was cut. This opening and several others undoubtedly primary, in which one to several of the more characteristic of the intolerant shrub and herb species occur, give good evidence that these species were plants of the sedgy openings and open pin oak areas. They have been almost eliminated within the forest by the gradual closing in of the trees, but have reproduced abundantly when and where the forest was cut but the land not tilled. In the utilization of forest areas for grazing, the openings suffered much. Furthermore, here were depressions where shallow but permanent ponds could easily be dug for water for the cattle. Thus often, the youngest places, successionally, have been most completely destroyed.

The soil on which these pin oak communities are found is the Clermont
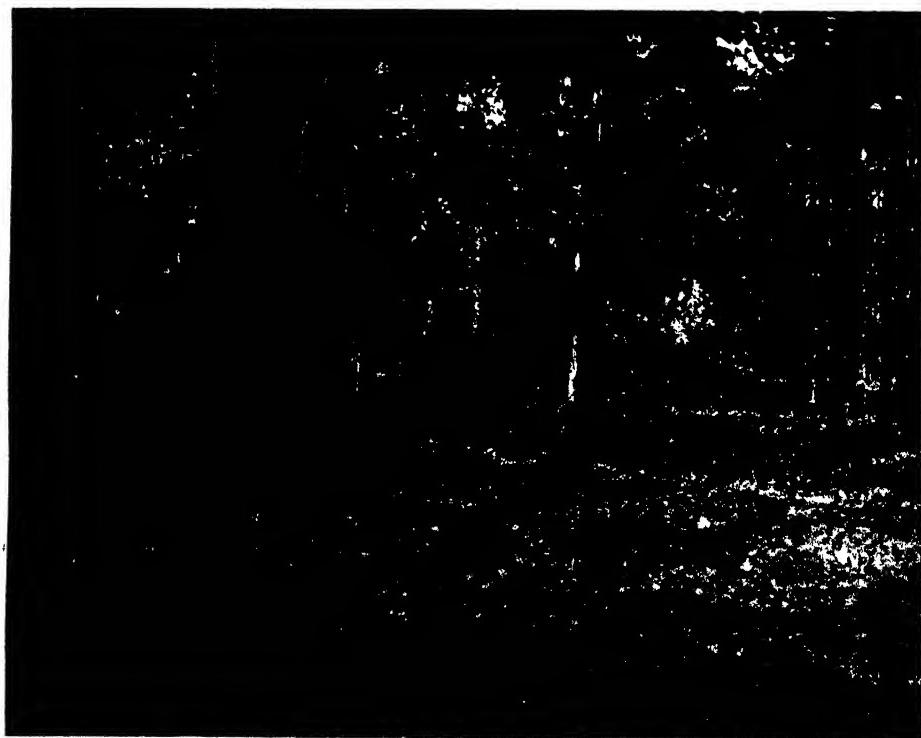
Fig. 7. A dense stand of small pin oak with some swamp white oak has changed this depression from an open pin oak-sedge community to a deep shade area almost without undergrowth. Though young, this pin oak stand is primary. One of the large trees of the depression, a swamp white oak, is seen to the left.

silt loam—the "white clay." The topographic relations may be seen from the transect, Fig. 30, which passes through two pin oak-sedge areas. The composition of the typical pin oak consocies is shown by area 1 (Table 2); it is this area which the transect, Fig. 30, crosses. Area 2 (Table 2) is successionally slightly older and hence contains a higher percentage of white oak.

Variations of the Pin Oak Consocies

Departures from the typical pin oak consocies occur, due to combinations of pin oak and other of the important trees of the associes or to local dominance of secondary species, as swamp white oak. Pin oak-sweet gum, pin oak-elm, and pin oak-red maple occur. Areas supporting these combinations are usually small in extent, scarcely noticeable depressions containing perhaps a dozen trees. They may, perhaps, be considered distinct segregates of the pin oak-red maple-elm-sweet gum associes, but they are relatively unimportant in the area as a whole. They are usually less open and less sedgy than the typical pin oak areas.

Red Maple, Red Maple-Elm, and Red Maple-Elm-Sweet Gum Associes-Segregates

Red maple is second in importance among the trees of depressions (Fig. 8). It, however, is not often associated in any considerable number with pin oak, but occurs separately, dominating the depression forest community, or with elm or elm and sweet gum. These forest communities may be open, without

FIG. 8. Large red maple in depression about two feet lower than surrounding beech woods. November.

ground cover, or is codominant with sedges (Fig. 12). In the sedge-grass mat, or locally supplanting it, *Ranunculus hispidus* var. *falsus, Phlox maculata* var. *odorata, Chelone glabra, Onoclea sensibilis, Polygonum arifolium, P. sagittatum, Viola cucullata, Lobelia cardinalis,* and other herbaceous plants and ferns are present (Fig. 13). Shrubs are few; *Ilex verticillata* and *Viburnum pubescens* var. *indianense* of the "characteristic shrubs" have been found, but none of the others. In denser stands, the sedge-grass layer is absent and very few herbaceous plants occur. Mosses are conspicuous.

In successionally older red maple depressions, beech is important in the understory foreshadowing its later co-dominance with red maple in the canopy of an intermediate forest stage. Where beech is present in depressions, its roots are very prominent on the surface of the ground, and arch upward sometimes 6 inches. The entire trunk may be elevated, the main roots then appearing as prop roots. Moss mats composed most commonly of Climacium, Thuidium, Polytrichum, Dicranum, Leucobryum and Sphagnum are especially prominent about the beech roots. *Mitchella repens* is abundant in such locations. If the trees are not too closely placed, *Impatiens biflora, Polygonum arifolium, P. sagittatum, Boehmeria cylindrica,* and other coarse herbaceous plants may occupy the depression.

The soil of the red maple depressions—or other communities in which
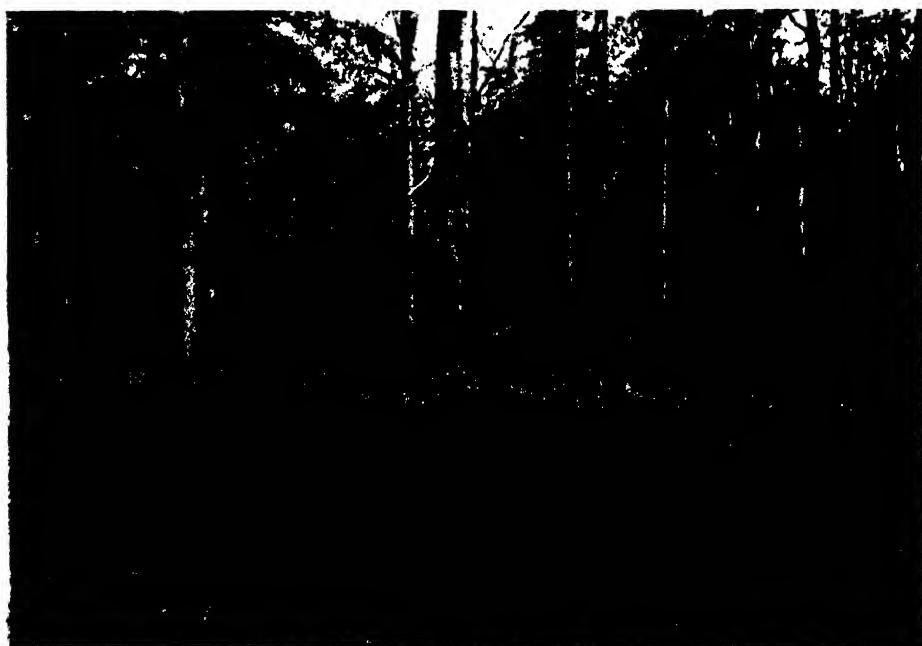
Fig. 12. Swamp forest in which the wood reed-grass, *Cinna arundinacea*, forms the ground cover. The trees are sweet gum, sour gum, and beech. Rice cut-grass, *Leersia oryzoides*, in and around the pool.

red maple is one dominant—is darker than in the pin oak depressions. That of many of these depressions is classified as Blanchester silt loam.

Area 4 of Table 2 gives the composition of the forest of one of the larger areas of the red maple-elm-sweet gum associes-segregate. The chart, Fig. 14A, is a representative plot in this area. The transect, Fig. 28 (in area 8 of Table 2), passes from a red maple-elm-sweet gum depression up to white oak-beech. The transect, Fig. 32, ends in a red maple depression in advanced stage of development—one in which beech is important in the understory.

2. RAVINE HEADS AND SHALLOW SWAMPY RAVINES

Certain of the indefinable depressions of the till plains, if followed radially in some direction, are seen to have outlets leading to shallow swampy ravines. Such ravine heads are just as imperceptible, topographically, as are the depressions, and bear much the same moisture relations to the surrounding flats. They are not to be likened to the beginnings of ravines working headward; their existence is due to inequalities in the drift surface, not to active erosion. The soil of these ravine heads is usually dark and referable to the Blanchester silt loam. Pin oak is not usually important; red maple or red maple and elm are almost always dominant. Carpinus as an understory to

Fig. 13. Buttercups, *Ranunculus hispidus* var. *falsus*, with scattered clumps of sensitive fern, *Onoclea sensibilis*, form a continuous ground cover in this swamp forest of red maple, elm, and sweet gum.

red maple is not unusual. In two areas—one in Warren County and one in Brown County—pumpkin ash *(Fraxinus profunda)* occurs.

Shallow ravines with definite valley flats and meandering and sometimes anastomosing sluggish streams traverse some of the upland areas. Such ravines have all the characteristics of old valleys and differ greatly from the V-shaped ravines cutting into the plain around its margin. They are, in fact, remnants of an older erosion cycle whose streams have not yet been rejuvenated. The valley flats of these streams support swamp forest of the same type as the glacial plain. White elm is always the most important tree, and with it may be a few other species as pin oak, shingle oak, and green ash (Fig. 33A). The forest of the slope is white oak-beech, an advanced successional stage. The transect, Fig. 32, crosses such a ravine in area 16 (Table 2).

B. Intermediate Forest Stages

The trees of the initial forest stages are, with the exception of sweet gum, intolerant; while they will reproduce for a time in open stands, they do not become established in closed stands even though no appreciable filling of depressions has taken place and hence no change in water relations. More tolerant species will enter, and some one of the intermediate stages develop. Hence forest communities of these intermediate stages may occupy depressions as deep and as wet as those occupied by initial forest stages.
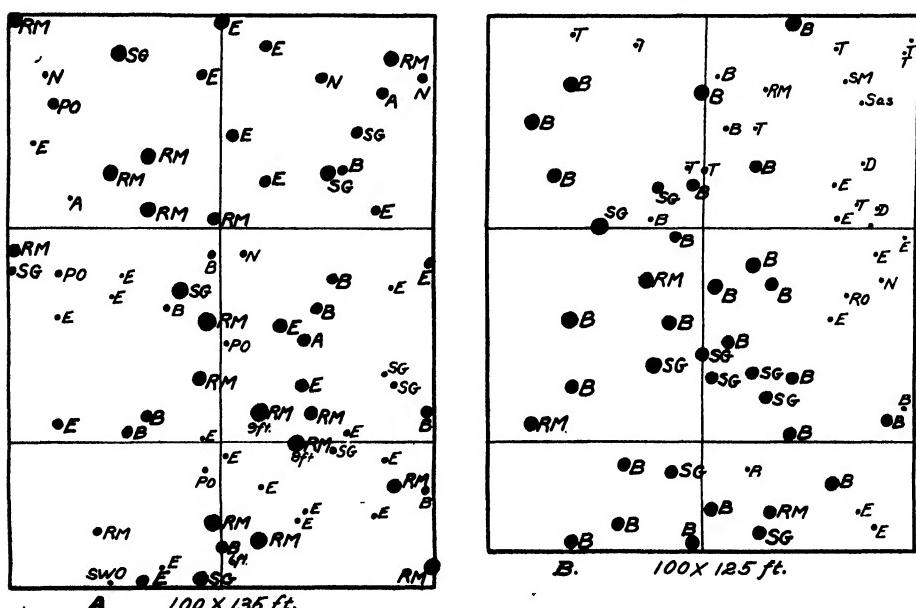
FIG. 14 (A). Representative plot in red maple-elm-sweet gum associes segregate.
   (B). Representative plot in beech-red maple-elm-sweet gum community. This plot is 150 feet from A and lies at a level 2.5 ft. above that plot. (For key to symbols see p. 129.)

A lowering of the water table, due either to gradual elimination of the depression by filling—a process which is so slow as to be almost negligible—or to stream dissection, permits the entrance of less hydrophytic trees and results in the development of intermediate forest stages. Decrease in light is then an auxiliary factor. Successions resulting either from lowered water table or decreased light or a combination of causes are similar, though in many instances beech increases in importance earlier in succession where decreasing light appears to be the most important causal factor.

The composition of the initial stage determines in part the composition of succeeding communities. White oak-pin oak or white oak forests (with or without an admixture of hickory)—forests of the type illustrated by areas 6 and 7 (Table 2)—succeed the pin oak consocies. Beech-red maple, beech-red maple-elm, or beech-red maple-elm-sweet gum—forests of the type illustrated by areas 8, 9, and 10 (Table 2)—succeed the initial forest stages in which red maple is important. A third developmental group is illustrated by areas 11, 12, and 13 (Table 2). The successional relationships are discussed later.

White oak always appears in intermediate stages in succession when pin oak was present in initial stages (see transect, Fig. 30; beech always enters early in succession when red maple was prominent in initial stages (see transect, Fig. 32). To what extent differences in successional trend are due to initial differences in the environment, to chance distribution and hence prior occupancy, or to the reactions of the initial species on the environment have not been determined. Red maple and elm usually occupy areas of Blanchester silt loam—a darker soil with higher organic content than the Clermont silt loam. Differences in the amount of nitrogen yielded in decomposition of different kinds of leaf litter have been demonstrated by Melin (1931). Lundegårdh (1931) also mentions the specific action of different kinds of decaying vegetation. Such differences are continuing and cumulative. Reactions of the occupying vegetation may be determinative as to the nature of later vegetation.

White Oak-Pin Oak Forest Community

The invasion of the pin oak consocies by white oak or hickory, or by white oak and hickory leads to the establishment of transition communities in which these trees are more or less codominant with pin oak. Most important of these transition phases is the white oak-pin oak forest in which hickory may be an important species; locally, pin oak and hickory dominate, the white oak entering later. Sweet gum may be present; if present in initial forest stages it reproduces and persists in the transition phase, forming a white oak-pin oak-sweet gum forest (Fig. 15). Swamp white oak continues as a secondary species of some importance; black oak enters with white oak. The composition of forests of this type is shown by areas 5 and 6 (Table 2).

The canopy of the white oak-pin oak forest is more continuous than is that of the typical pin oak opening. Usually, saplings are more numerous in the understory and the forest as a whole is dense. Sedges drop out, as do all of the sun swamp plants of the pin oak areas. Of the shrubs, only *Ilex verticillata* and *Viburnum pubescens* var. *indianense* remain. Herbaceous plants are few. This forest is distinctly a transitional step in the establishment of the white oak or white oak-hickory forest.
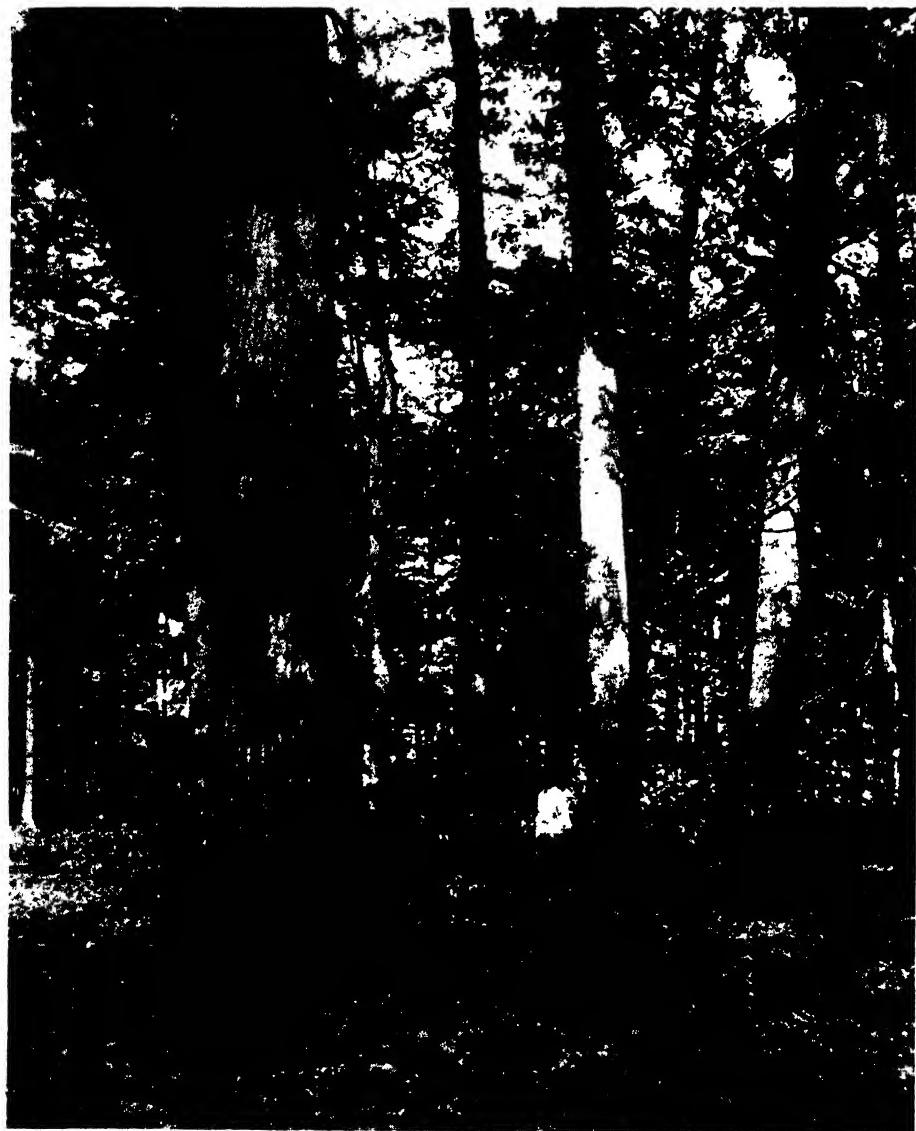
Fig. 15. White oak-pin oak-sweet gum forest in which smaller beech trees are present. This is in a low part of area 13 (Table 2).

White Oak or White Oak-Hickory Associes

White oak may dominate over large areas, forming a long-lived community occupying a definite position in succession (Figs. 16, 17). Shellbark hickory may or may not be important. Locally, small groves of white oak occur in areas of mixed forest (see parts of transects, Figs. 30, 32); these, too, appear to occupy a definite successional position, rather than to represent local segregates or consocies of a mixed forest community.

The white oak consocies varies from a dense forest with a young tree understory and poor herbaceous ground layer (the usual condition) to an open forest of park aspect with openings in which a grass-sedge ground cover is well developed (Fig. 16). The more open parts occupy depressions, places usually dominated by pin oak. Pin oak and swamp white oak may be here in small numbers, and may even be present in the understory. Such open white oak areas contain some of the typical shrubs and herbaceous plants of pin oak openings. More typically, the white oak forest is a closed community with an understory of fairly tolerant and tolerant species. Area 7 (Table 2) is such a white oak forest with an understory in which white oak is the most important species and shellbark hickory, black oak, beech, dogwood, serviceberry *(Amelanchier canadensis)*, elm, red maple, and swamp white oak are

FIG. 16. White oak forest, with park-like openings. September.

also present (Fig. 17). In other areas successively older, hickory and beech or beech are most important in the understory.

The Beech-Red Maple-Elm-Sweet Gum, Beech-Red Maple, and Beech-Red Maple-Elm Communities

The invasion of beech in the red maple, red maple-elm, or red maple-elm-sweet gum associes-segregates results in intermediate stages in which the constituent species are mixed in all proportions, or in some instances, in a forest in which beech reaches an importance amounting almost to dominance. The commingling of all species is illustrated by forest area 8 (Table 2)—within the finest virgin stand of mixed forest on the till plain (Figs. 10, 11, 13, 18A, 18B, 19, 21, 26, 29A, 29B). All gradations from the more open depressions (Fig. 11) and sweet gum swamps (Fig. 10) to the beech climax forest (Fig. 26) are discernible in this forest. Much of the forest is, however, a mixed stand of beech, red maple, elm, sweet gum, with locally, white oak, hickory and sour gum (Figs. 18A, 18B, 19).

Beech in wet places in these intermediate forest communities shows the adaptability of its root system and behaves as do the occasional beech trees in red maple depressions. Fine roots form a thick mat in the upper few inches of soil. These intermediate stages in which beech is prominent assume early the deep shade conditions characteristic of the climax stands. This, together

Fig. 17. White oak forest with understory of tolerant species. This is in area 7 (Table 2). November.

with root competition due to the superficial position of beech roots, acts to prevent the entrance of white oak in this sere. A selected plot in this community is shown in Fig. 14B; this plot is 150 feet from the plot of the red maple-elm-sweet gum associes-segregate shown in Fig. 14A and lies at a level 2½ feet above that plot.
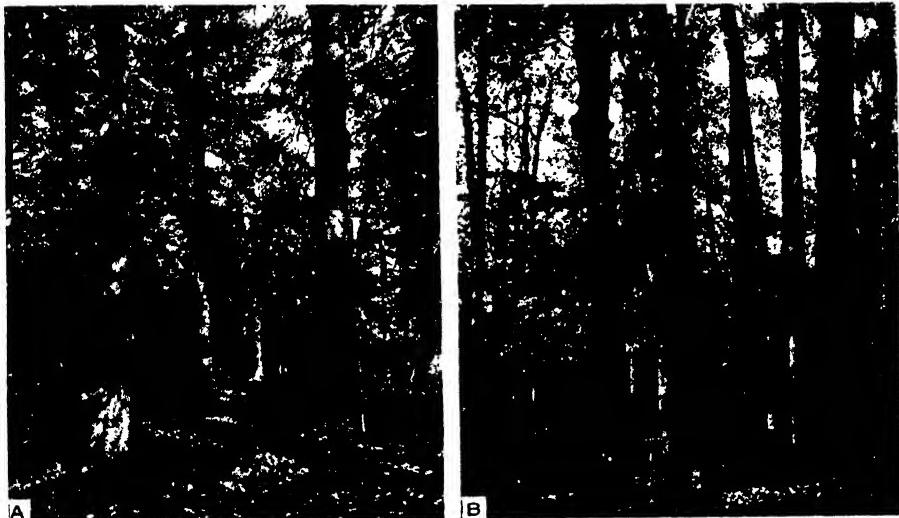
Fig. 18 (A). A mixed forest with elm (left) and pin oak (right) in foreground and beech and white oak beyond; in forest area 8 (Table 2).

(B). Beech, red maple, elm, and sweet gum, constituents of intermediate stages, in a compact group in forest area 8 (Table 2).

Fig. 19. A mixed stand with beech, red maple, elm, sweet gum, and shellbark hickory; in area 8 (Table 2).

The undergrowth is made up of canopy species and occasional tulip trees, sugar maple and red oak. Spice bush *(Benzoin aestivale)* is an important shrub and introduces something of the climax aspect. The herbaceous plants are few. Mosses are much less conspicuous than in earlier stages.

Beech-White Oak-Sweet Gum, Beech-White Oak-Red Maple, and Beech-White Oak-Red Maple-Sweet Gum Communities

Beech-white oak-sweet gum or beech-white oak-red maple-sweet gum succeed the initial pin oak-red maple-elm-sweet gum associes; or, beech-white oak-sweet gum may develop from the pin oak-sweet gum, or even from the red maple-elm-sweet gum associes-segregate. The high crowns of sweet gum admit more light to the understory than do those of red maple and elm, hence the admixture of sweet gum in initial forest stages makes possible the later entrance of white oak in any succession in which sweet gum is initially present, even though pin oak may be absent.

Beech-white oak-red maple, developmentally, is derived only from the pin oak-red maple—a community of unusual occurrence. However, the beech-white oak-red maple community appears sometimes to succeed other initial stages in which red maple is important and pin oak absent (see Fig. 32). In such instances, it occupies positions intermediate between successions developing from unlike initial stages, as illustrated by Fig. 20. When in two adjacent depressions the initial stages are different, apparent inconsistencies in order of successional stages occur. A profile such as is represented by Fig. 20 (with the distribution of forest communities indicated by initials) illustrates
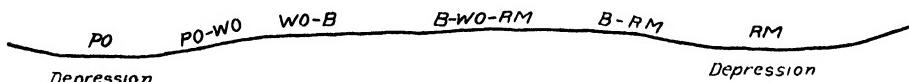
FIG. 20. Commingling of communities derived from unlike initial stages.

this point. Of all the communities represented, white oak-beech is successionally most advanced. Yet there is little reason to believe that white oak-beech will succeed the beech-white oak-red maple. Rather, both may in time give way to beech. Two successions are here in progress: (1) pin oak → pin oak-white oak → white oak-beech → beech and (2) red maple → beech-red maple → beech. An intermingling of communities occurs in the zone of contact resulting in the beech-white oak-red maple community which is not to be interpreted as a developmental stage following beech-red maple.

The beech-white oak-sweet gum and beech-white oak-red maple-sweet gum communities occur only in the southern half of the area, because of the limitation in range of sweet gum. The wide range of tolerance of sweet gum permits its continuance in succession to late intermediate stages. Statements made by Cheney (1929) concerning the extreme intolerance of this species are not applicable in the area under consideration. It does reproduce in the
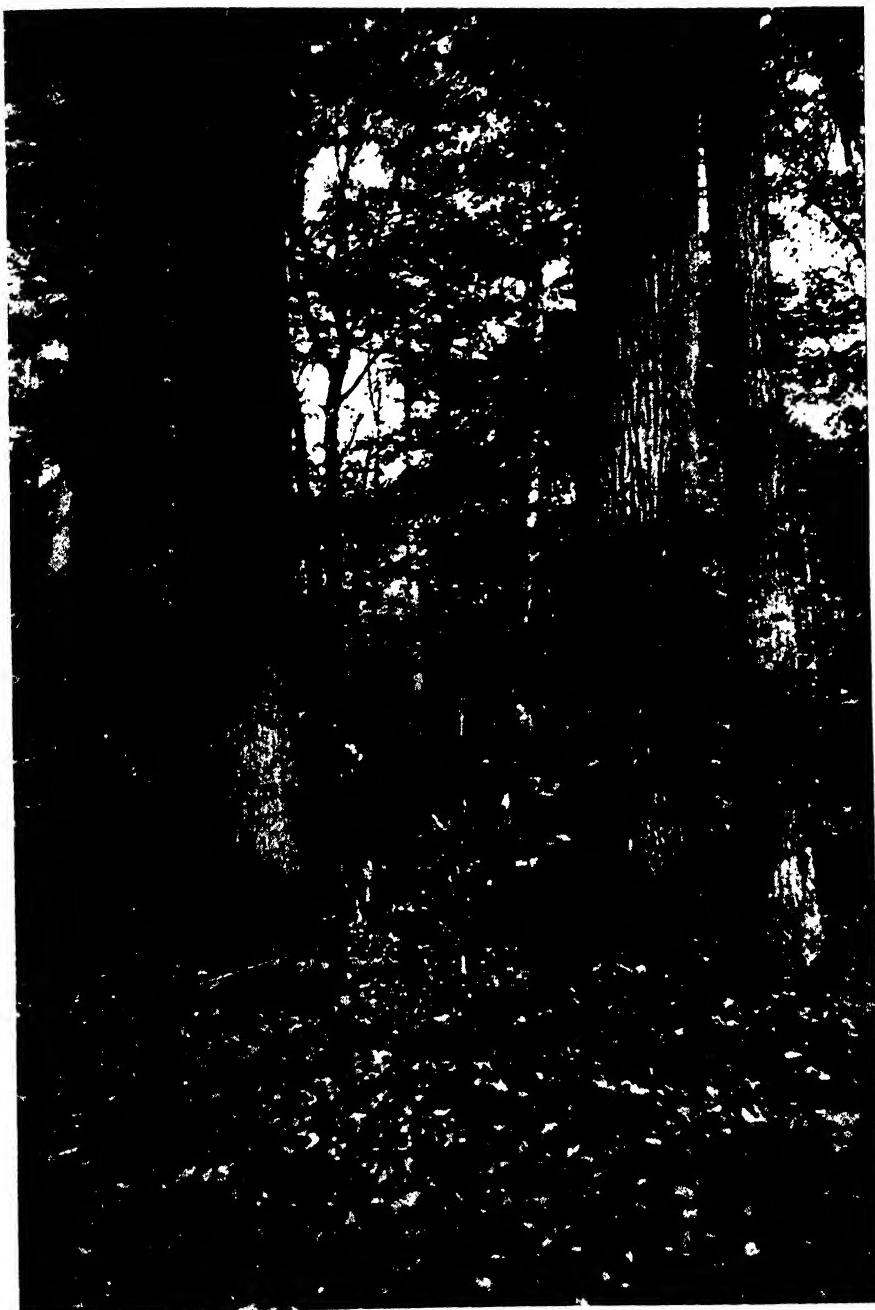
FIG. 21. Large sweet gum trees in forest of intermediate successional stage. Large tree to right is 9 ft. 3 in. in circumference, b.h.

mixed forest of intermediate stages (see Fig. 22), there growing tall and slender and pushing up into the light (Fig. 21) and is never dominant in any forest in which it occurs, except in some relatively small areas of second growth stands.

The proportions of the dominants in these three communities may vary considerably. Other trees of the initial and earlier intermediate stages, as elm, pin oak, sour gum, and shellbark hickory, may be present. The undergrowth contains, in addition to the species of the canopy, Carpinus and an admixture of mesophytic species as dogwood, tulip tree, sugar maple, mulberry, wild cherry, and white ash. Elderberry *(Sambucus canadensis)*, papaw *(Asimina triloba)*, and spice bush *(Benzoin aestivale)* are often present. Among the few and usually scattered herbaceous plants are: ferns *(Aspidium noveboracense, Asplenium angustum, Onoclea sensibilis, and Botrychium obliquum)*, partridge berry *(Mitchella repens)*, pipsissewa *(Chimaphila maculata)*, red touch-me-not *(Impatiens biflora)*, May apple *(Podophyllum peltatum)*, and cucumber-root *(Medeola virginica)*. The soil here is looser than in earlier stages and generally covered with a light leaf litter.

A chart of a selected plot in the beech-white oak-sweet gum community (approaching beech-white oak) is shown in Fig. 22. This is within area 12 (Table 2).

C. Late Successional Stages

Late in successional development and with approach toward a climax stage, the number of forest communities decreases so that not more than two
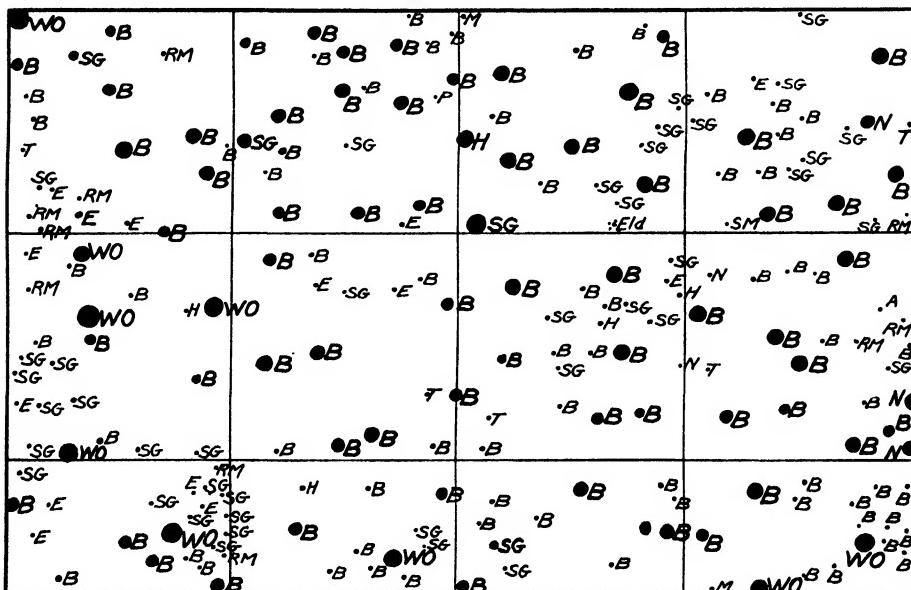
Fig. 22. Representative plot (130 x 200 ft.) in advanced stage of beech-white oak-sweet gum community; in forest area 12 (Table 2). (For key to symbols see p. 129.)

or three are recognizable: the white oak-beech associes, by far the most important; a variant of this, a forest of beech and white oak in which beech is dominant and white oak secondary; and a beech or beech-ironwood forest community. Each may ultimately develop into the beech climax forest, if dissection does not destroy the plain before the developmental series reaches its culmination.

White Oak-Beech Associes

A white oak-beech forest, with a scattering of the more hydrophytic species of earlier successional stages and of mesophytic species, is the most advanced stage in forest development reached over much of the till plain. In the associes as such white oak and beech in nearly equal numbers form about 90 per cent of the stand, with shellbark hickory, ash, black and red oak, and sour gum as secondary species (Fig. 23). However, in any given forest tract the inclusion of small groups of more hydrophytic species reduces the percentage of white oak and beech from 90 to 60 or 75. Pin oak, swamp white oak, elm, and red maple occupy the depressions or shallow ravine heads and are remnants of earlier successional stages. Areas 14 to 17 (Table 2) are representative of the white oak-beech forest; for one area, no. 14, the distribution of secondary and hydrophytic species is illustrated in the transect, Fig. 30. In the best examples of the white oak-beech forest (as area 17), the aspect from a distance is of a white oak forest. This tree dominates because of its greater size and height, here reaching its largest size, 10 to 14½ feet in circumference, b.h. In such forests (Figs. 23, 24) beech, though

FIG 23. Typical white oak-beech forest, in which white oak and beech are present in about equal proportions, but in which white oak towers well above the beech. In forest area 17 (Table 2.)

large, forms something of a lower story beneath the white oak. Generally, in the white oak-beech associes, beech varies from year old seedlings to trees 10 feet in circumference. Locally, beech is dominant (Fig. 25) and in these places is larger than elsewhere; locally white oak, even numerically, dominates (Fig. 24) where beech trees are smaller. The largest beech trees occupy the oldest topographic situations—the edges of the almost imperceptible ravines and the ridges. Hydrophytic herbaceous species have disappeared; *Ilex verticillata* and *Viburnum pubescens* var. *indianense* may be present, though never abundant nor vigorous; more mesophytic species, especially spice bush, become abundant. The herbaceous layer is still poor; a very few common species of mesophytic forests have entered, as *Podophyllum peltatum*, *Phlox divaricata*, and rarely *Eupatorium urticaefolium*. The best areas of the white oak-beech forest (as far as canopy is concerned) are badly grazed by hogs and very little undergrowth remains.

Beech is reproducing much more abundantly than white oak; the indication from the composition of half-grown trees is that a beech forest will in time succeed the white oak-beech forest. This is substantiated by the greater dominance of beech in situations in which succession has progressed most rapidly.

The typical white oak-beech forest is one in which these two species are present in about equal proportions, with beech becoming dominant as succession progresses. The forest with beech a dominant is a transition phase between the white oak-beech associes and the climax beech forest. However, in some areas a beech-white oak forest occurs which seems never to have had a high percentage of white oak.

Fig. 24. White oak-beech forest where white oak numerically exceeds beech; here beech trees are smaller than in the typical white oak-beech associes. In forest area 17 (Table 2.)

Sugar maple may be present in the understory of the white oak-beech forest or codominant with beech in that layer. This is always true at the margin of the till plain and on the gentle slopes of stream headwaters. This points to the possible terminal—though not climax—position of the white oak-beech associes. A forest community of the till plain will be replaced by one of the slope series. This is indicated by zonations in which the white oak-beech forest of flats passes almost imperceptibly into a beech-sugar maple-white oak forest of slopes, or the beech-white oak forest into a beech-sugar maple slope forest (see transect, Fig. 34). This is a step toward the regional climax, but not a stage in the developmental succession in progress here. The developmental succession—white oak-beech → beech—is clearly indicated in many places, both by understory and zonation.

Beech or Beech-Ironwood Associes

Beech enters early in successions in which red maple is important in the initial stages. This results in the early dominance of beech, at first with red maple in the beech-red maple intermediate stage, later in a forest in which red maple still persists, although it is unimportant. This beech forest—a late developmental succession—white oak-beech → beech—is clearly indicated in —shares with other developmental stages of the till plain successions, the

FIG. 25. Beech dominates in local areas in the white oak-beech forest; here beech trees are larger than in the mixed parts of the stand. Figs. 24, 23, and 25, all from the same forest area, indicate clearly the successional development in progress.

features imparted by the admixture of somewhat hydrophytic herbs and the
moss or moss-lichen mats about exposed tree roots.   Beech roots here have the
superficial habit which characterizes them throughout all hydric stages.   In
many places, ironwood *(Carpinus caroliniana)* is an important or dominant
member of the understory.   Such communities frequently occupy the inde-
finable depressions at ravine heads; the soil seems usually to be the Blanchester
silt loam.   A change to less wet conditions results in a change in understory, if
not in canopy, and leads to the establishment of the beech climax forest, be-
tween which and the beech-red maple forest, this community is transitional.

D. Beech Forest: A Physiographic Climax or Subclimax

A beech forest is the usual type near the margins of the upland plains,
where the beginning of dissection has lowered the water table slightly, on
smaller remnants of the till plain, on the yellowish Rossmoyne silt loam, and
locally on dark soil in the undissected plain.   The beech forest contains fewer
species than most of the other forest communities of the till plain, and is
characterized by the marked dominance of beech, which comprises 80 to 90
per cent of the forest stand (Figs. 25, 26).   Forests having much the aspect
of this beech forest have been at times produced by the cutting of white oak
in the white oak-beech associes (Fig. 27) ; this should not be confused with
the true beech association.   Some areas of the beech association are succes-

Fig. 26. Beech forest—the physiographic climax or subclimax of forest development
on the till plain.

sionally related to the white oak-beech forest and represent the final dominance of beech, the most tolerant species of the forest of the till plains. Other areas appear not to have passed through a white oak-beech stage, but rather to represent the culmination in development in the red maple succession. These are apt to contain remnants of red maple, whose wide range of tolerance makes it possible for it to persist through the entire succession in which it is originally prominent. Areas 18 and 19 (Table 2) show the composition of the beech association; area 19 lies closer to the margin of the upland plain, hence has felt more the influence of dissection and contains fewer red maples.

The understory of the beech forest differs from all other communities in the greater prominence of those mesophytic species which are common in the regional climax. Beech is always prominent in the understory, and with it sugar maple, white ash, and dogwood, which emphasize the relationship to the mixed mesophytic forest. Papaw, spice bush, elderberry, and Carpinus are also usually present. White oak may be represented in the understory in less dense places and points to the appearance of white oak in the mixed mesophytic forest of the slopes.

The herbaceous layer is poor, but contains a few of the plants of the mixed mesophytic forest as *Eupatorium urticaefolium, Circaea lutetiana, Amphicarpa monoica, Podophyllum peltatum*, and *Viola eriocarpa*. Virginia creeper

FIG. 27. Beech forest produced by the cutting of white oak from a white oak-beech associes. Such forest closely resembles the beech climax association.

Grape—wild grape, *Vitis cordifolia*
H—shellbark hickory, *Carya ovata*
Ha—white-heart hickory, *Carya alba*
Hc—bitternut hickory, *Carya cordiformis*
Hp—pignut hickory, *Carya glabra*
Ilex—winterberry, *Ilex verticillata*
M—mulberry, *Morus rubra*
RM—red maple, *Acer rubrum*
SM—sugar maple, *Acer saccharum*
N—sour gum, *Nyssa sylvatica*
BO—black oak, *Quercus velutina*
PO—pin oak, *Quercus palustris*
RO—red oak, *Quercus rubra*
ShO—shingle oak, *Quercus imbricaria*
SWO—swamp white oak, *Quercus bicolor*
WO—white oak, *Quercus alba*
O—hop hornbeam, *Ostrya virginiana*
P—wild cherry, *Prunus serotina*
Pa—papaw, *Asimina triloba*
P. ivy—poison ivy, *Rhus Toxicodendron*
Rasp—raspberry, *Rubus occidentalis*
Rb—redbud, *Cercis canadensis*
Rose—climbing rose, *Rosa setigera*
Rosa car.—swamp rose, *Rosa carolina*
Sas—sassafras *Sassafras variifolium*
Sbn—*Smilax Bona-nox*
Sp, Spice—spicebush, *Benzoin aestivale*
Syc—sycamore, *Platanus occidentalis*
SG—sweet gum, *Liquidambar styraciflua*
T—tulip tree, *Liriodendron tulipifera*
V—black haw, *Viburnum prunifolium*
Vd—arrow-wood, *Viburnum pubescens* var. *indianense*
W—walnut, *Juglans nigra*
oblique dashes—poison ivy, *Rhus Toxicodendron*
single vertical dashes—wood reed-grass, *Cinna arundinacea*
groups of vertical dashes—*Carex spp.*

A transect 200 feet long and 75 feet wide (Fig. 28) in a depression in an ungrazed virgin forest in Highland County (area 8 of Table 2) passes from an advanced red maple-elm-sweet gum stage through beech-red-maple-elm-sweet gum and beech-white oak. There is a rise of only one foot in 150 feet in this transect. The white oak is probably older than the other trees—except perhaps some of the red maples. Sedges and grass *(Cinna arundinacea)*, *Onoclea sensibilis*, and *Phlox maculata* var. *odorata* are the most important herbaceous plants of the open forest of the depression; other species present are *Chelone glabra*, *Ranunculus hispidus* var. *falsus*, *Polygonum arifolium*, *Solidago rugosa*, *Agrimonia parviflora*, *Scutellaria lateriflora*, *Boehmeria cylindrica*, *Lobelia cardinalis*, *Viola cucullata*, *Thalictrum*
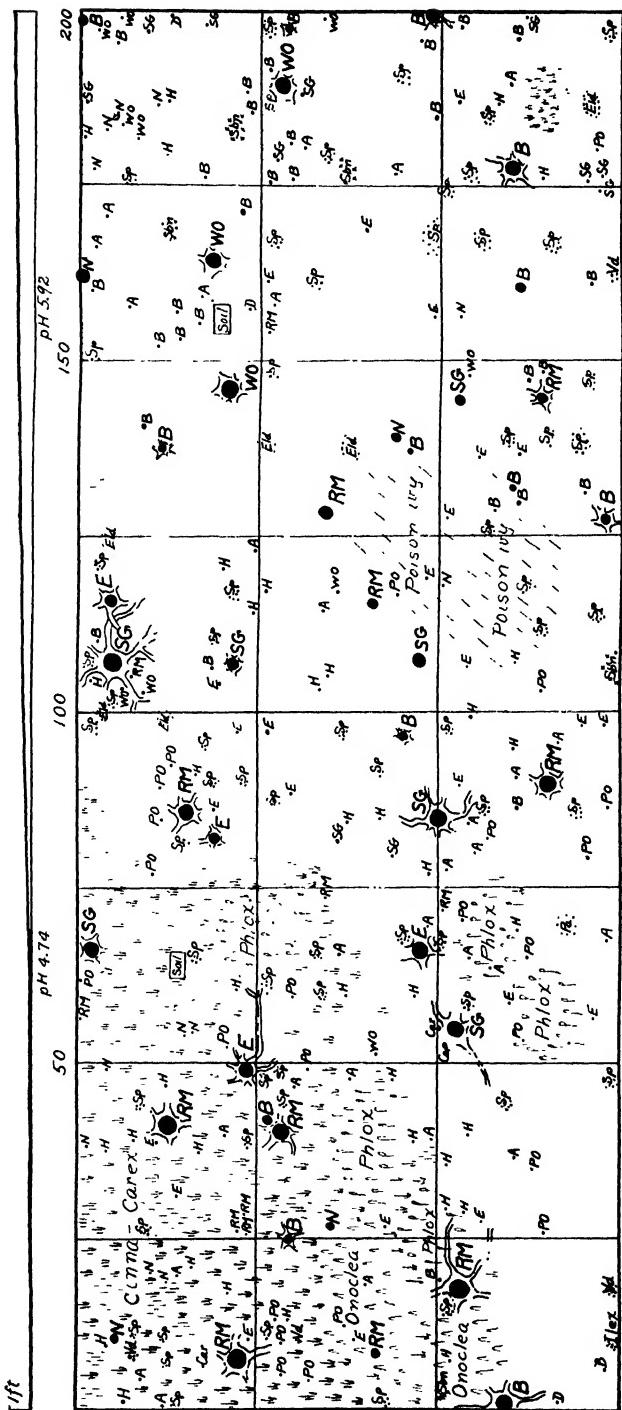
FIG. 28. Transect 200 feet long and 75 feet wide from red maple-elm-sweet gum through beech-red maple-elm-sweet gum to beech-white oak.

FIG. 29 (A). Red maple, elm, and sweet gum in lower portion of area of transect,
Fig. 28. October.
    (B). Beech, elm, and two sweet gums, with white oak and beech beyond; slope and
rim of depression traversed by transect, Fig. 28. October.

purpureum, Penthorum sedoides, Mimulus ringens, Ludvigia palustris, Impatiens biflora, and *Ilysanthes dubia.* Shrubs in the depression include *Ilex verticillata, Viburnum pubescens* var. *indianense, Benzoin aestivale, Smilax Bona-nox,* and *Rhus Toxicodendron.* The composition of the understory is shown in the transect; species of the initial forest stages continue to dominate. In the beech-red maple-elm-sweet gum part of the transect, poison ivy becomes much more prominent; elderberry enters and spicebush becomes more abundant. The sedges and grass and most of the herbaceous plants mentioned above drop out. Beech becomes more plentiful in the understory. In the beech-white oak part, all trees of the initial stages are absent in the understory except hickory and an occasional sweet gum. Dogwood has appeared. Figures 11 and 29A, 29B show the aspect of the vegetation. Other parts of the same forest tract are illustrated by Figures 10, 13, 18A, 18B, 19, 21 and 26.

A transect 1,200 feet long and 50 feet wide (Fig. 30) traversing areas 1 and 14 (Table 2) demonstrates the sequence of communities in the pin oak → white oak → beech succession. The total relief is 4 ft. 8 in. For 200 feet the transect passes through a typical pin oak opening with a continuous sedge ground cover except under the one beech tree. *Ranunculus hispidus* var. *falsus, Cardamine bulbosa,* and *Phlox maculata* var. *odorata* are scattered among the sedges. *Rosa setigera* is the only shrub present. There are very few small trees. On the slopes of the depression, still within the pin oak consocies, saplings become abundant and point to the formation of a denser stand and the elimination of the sedge ground cover. A transitional belt of hickory *(C. ovata* and *C. alba)* with black oak intervenes between the pin oak and the white oak-hickory stages; this does not have a sedge ground cover. Beech becomes prominent in the understory of the white oak-hickory forest, continuing through the white oak-beech into the beech area. The last 150 feet passes down into another but shallower depression occupied by pin oak with an admixture of black oak and white oak. Saplings are abundant but not yet large enough to shade out the sedges. Figure 31 A, B, C, D shows the aspect of communities along the transect.

The influence of broad shallow ravines with old streams not yet rejuvenated is demonstrated by a transect 1,050 feet long (Fig. 32) crossing such a ravine and the adjacent flat and ending in a very shallow depression. The total relief is 16 feet. The ravine flat, in which is a shallow anastomosing stream, is occupied by an elm-pin oak community (20 to 80 ft.); the adjacent ravine slopes by white oak with sugar maple and dogwood prominent in the understory, a mesophytic character correlated with dissection of the plain (80 to 240 ft.). A white oak-beech community with beech, sugar maple, and dogwood in the understory occupies the very gentle upper slopes and margin of the plain (240 to 550 or 600 ft.). On the flat, the forest is beech-white

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FIG. 30. Transect 1,200 feet long and 150 feet wide illustrating the pin oak → white oak → beech succession.
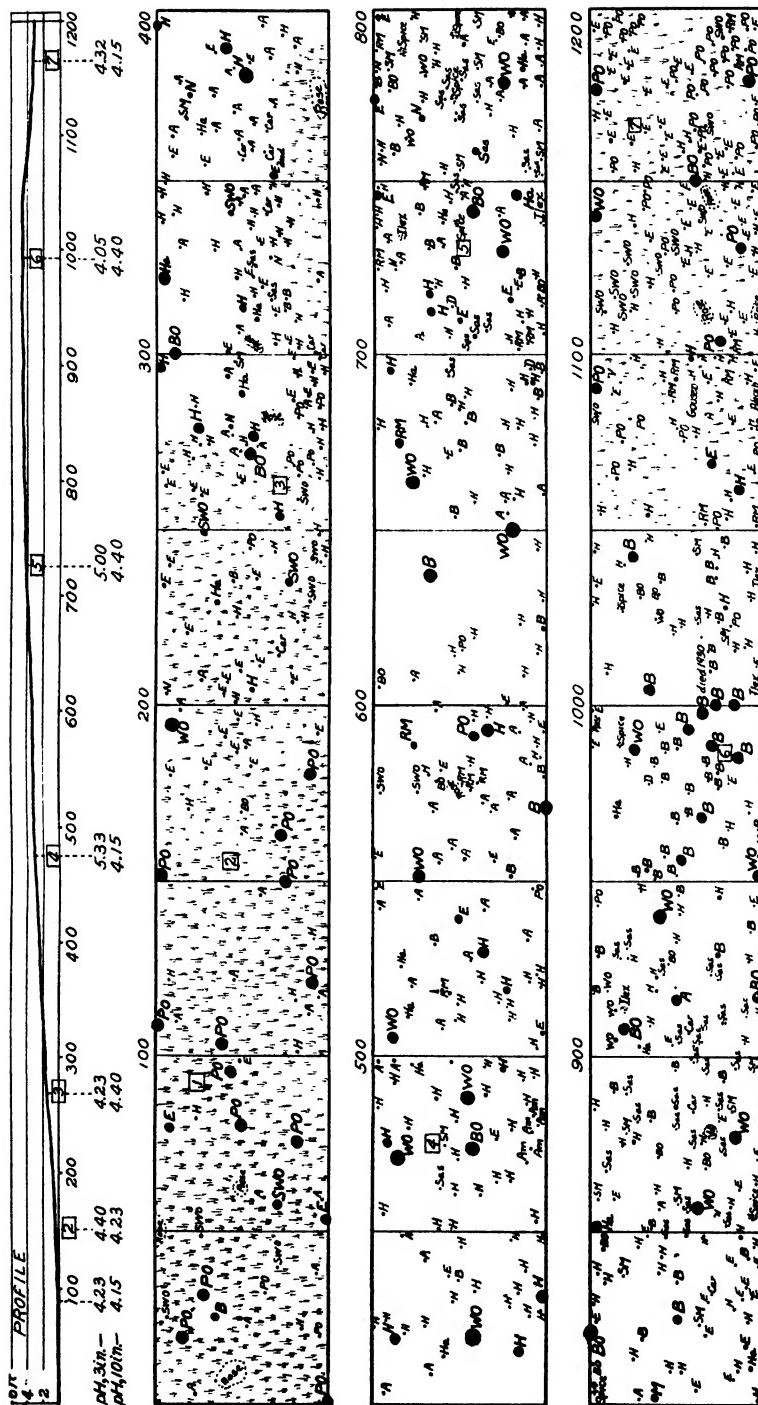
FIG. 31. Forest communities along transect, Fig. 30.
    (A). Pin oak-sedge area with large shellbark hickory to left.
    (B). White oak with black oak (right) and shellbark hickory (center right).
    (C). White oak-beech.
    (D). Beech.
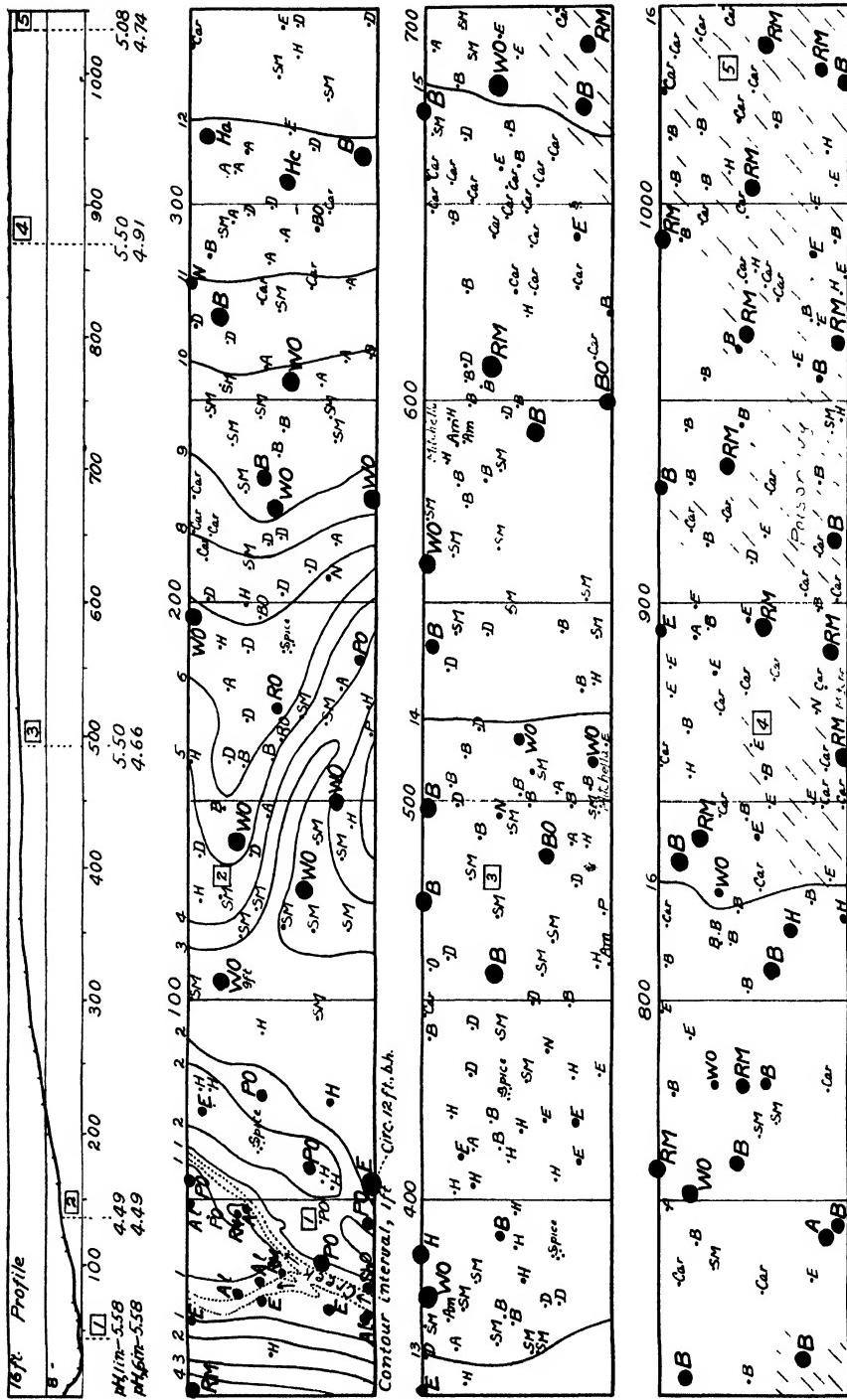
Fig. 32. Transect 1,050 feet long and 50 feet wide to show influence of broad shallow ravines.
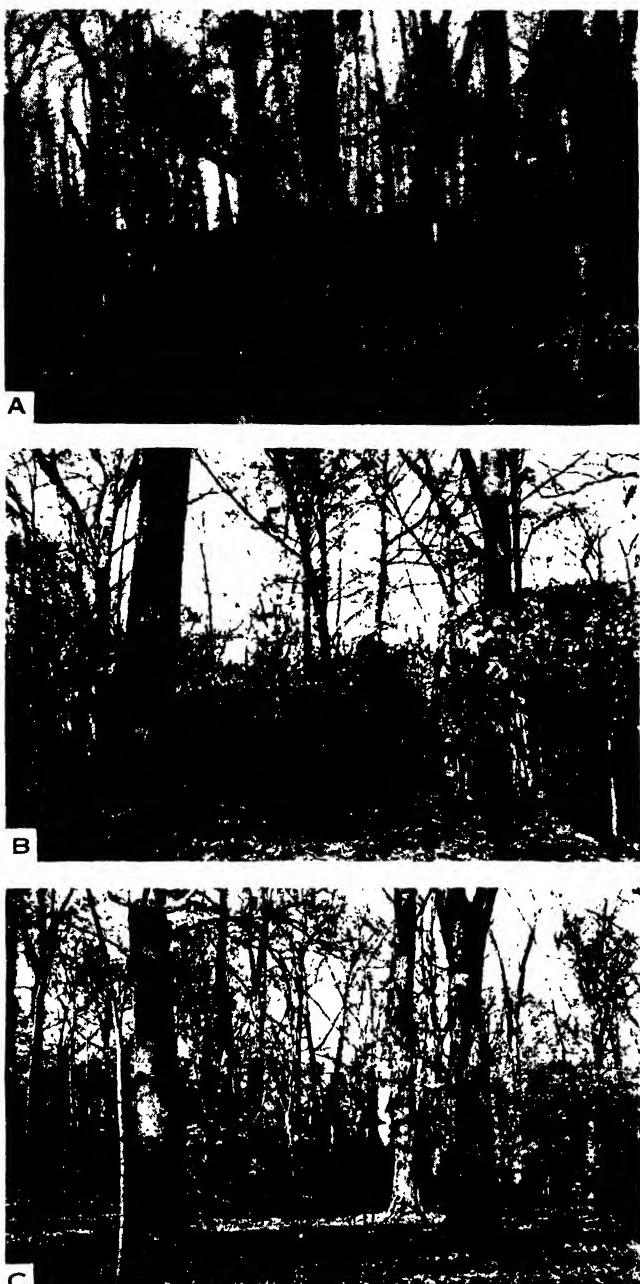
Fig. 33. Aspect of forest along transect, Fig. 32.
November.
   (A). In swamp forest of shallow ravine flat.
   (B). In white oak-beech at top of slope.
   (C). In beech-red maple of shallow depression.
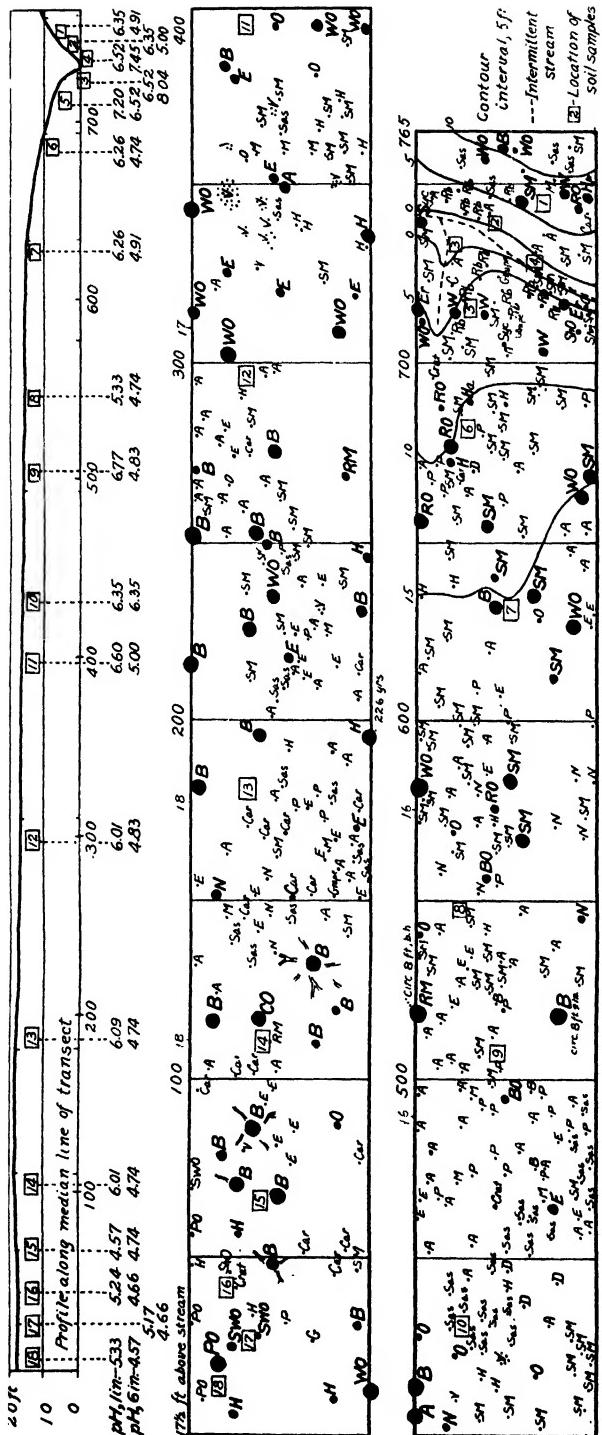
Fig. 34. Transect 765 feet long crossing a V-shaped ravine cut in till plain.

oak-red maple with beech and Carpinus most prominent in the understory and occasional Amelanchier; poison ivy forms an almost continuous ground cover; *Mitchella repens* is present (600 to 800 ft.). Beech-red maple, with beech and Carpinus in the understory, occupies the wet flat (800 to 1,050 ft.). This transect illustrates the intermingling of communities of two different successions, as discussed in connection with Figure 20. The aspect of communities of this forest is shown by Fig 33 A, B, C.

More pronounced stream dissection with V-shaped ravines of eroding streams, permits the entrance on the ravine slopes of a variety of trees of the mixed mesophytic forest. A transect (Fig. 34) crossing such a ravine which is cut 16 feet below the adjacent plain shows the influence of dissection on the forest of the flat and the nature of the slope forest. The beech-sugar maple forest of the slope (with other mesophytic species) changes abruptly to a beech-red maple forest just back of the margin of the flat. Less than 600 feet from the stream beech is of the swamp forest type with roots spread upon the surface of the ground and 700 feet from the stream a depression only 6 inches below the level of the plain contains such swamp forest species as pin oak and swamp white oak. It will be noted that the soils of the ravine slopes are for the most part circumneutral; those of the flat and slight depression acid; and that the most acid soils are those of the depression.

IV. SECONDARY VEGETATION

The secondary vegetation of the till plains is made up of herbaceous and shrub meadow communities and forest. Locally, small and shallow ponds, frequently intermittent, introduce communities of hydrophytes (Fig. 35). Many of these ponds are partly artificial and were made by the deepening of depressions which doubtless originally contained ponds.

Ponds and Wet Meadows

In the intermittent and shallow ponds few aquatics occur. Amphibious and swamp plants are most abundant and include:

Eleocharis obtusa	*Alisma subcordatum*
Eleocharis capitata	*Lophotocarpus calycinus*
Scirpus cyperinus	*Sagittaria latifolia*
Scirpus atrovirens	*Typha latifolia* (very rarely)
Carex (species of pin oak openings)	*Ranunculus laxicaulis*
Juncus effusus	*Ranunculus pusillus*
Juncus marginatus	*Penthorum sedoides*
Juncus brachycarpus	*Callitriche heterophylla*
Juncus acuminatus	*Ludvigia palustris*
Leersia oryzoides	*Mimulus alatus*
Glyceria septentrionalis	
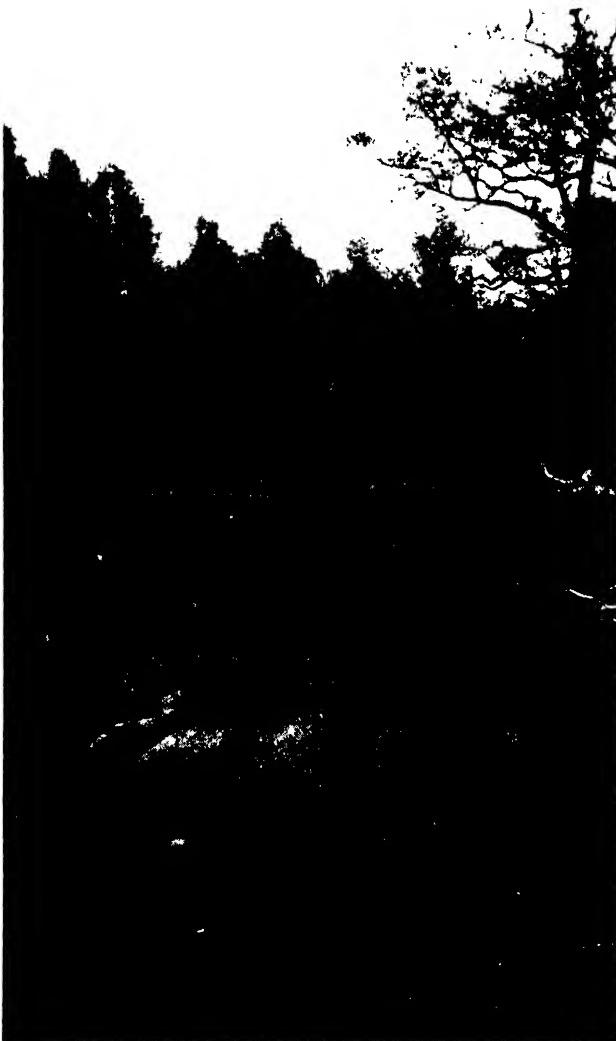
FIG. 35. Shallow pond in till plain around which Eleocharis and Juncus, Carex and Scirpus, *Rosa setigera* and *R. carolina*, and pin oak form successive zones leading to the primary forest which is close by and to which the large white oak on the right belongs.

Only a few of these are limited to ponds or pond margins. The marginal swamp plants of ponds may be the pioneers of wet flats. These secondary swamps contain many plants not seen in primary forest openings; these are the common and rather widespread hydrophytes. A few species only, as *Lophotocarpus calycinus*, the two species of Ranunculus, and some of the sedges and rushes, are in this general region limited to the till plain. These occur in primary as well as secondary areas.

Meadow Communities

Meadow communities are extensive. Some have occupied land formerly tilled; others have followed cutting on land never agriculturally utilized. Meadows on the yellowish Rossmoyne silt loam, on the dark Blanchester silt loam, and on the white clay or Clermont silt loam differ decidedly from one another. On the Clermont silt loam the greatest variety of species is seen and only on this soil do the more characteristic plants of the till plain become abundant.

Meadows dominated by *Andropogon virginicus* are the general type on the Rossmoyne silt loam. Such meadows usually contain, in addition to the Andropogon, a few other grasses *(Agrostis perennans, Eragrostis pectinaceus, Aristida gracilis, A. purpurea), Polygala sanguinea, Solidago nemoralis,* and *Gnaphalium polycephalum.* In areas recently tilled the latter two plants may dominate. Some shrub and tree invasion is usually evident; dewberry *(Rubus trivialis)* and blackberry *(Rubus frondosus)* are the common shrubs; Sassafras is the most abundant tree invader; with it may be a number of other species as white elm, hickory, and sour gum.

The meadows of the Blanchester silt loam areas are without characteristic plants; they are usually weedy ruderal communities which may contain some swamp plants.

The white clay or Clermont silt loam supports herbaceous and shrub meadows floristically distinct from other communities. Recently abandoned tilled land is usually occupied by Aristida, either *A. gracilis* or *A. purpurea* (Fig. 36). Land which has not been tilled or long-abandoned tilled land adjacent to untilled land is occupied by a variety of herbaceous plants; grasses and sedges are not dominant except in depressions where the wet meadow vegetation prevails. More abundant or characteristic herbaceous plants are:

Aspidium thelypteris	*Sabatia angularis*
Panicum clandestinum	*Gentiana Saponaria*
Scirpus cyperinus	*Mimulus alatus*
Lilium canadense	*Chelone glabra,* and var. *elongata*
Habenaria peramoena	*Lobelia cardinalis*
Spiranthes cernua	*Eupatorium perfoliatum*
Polygonum sagittatum	*Eupatorium maculatum*
Apios tuberosa	*Solidago rugosa*
Viola cucullata	*Solidago canadensis*
Viola lanceolata	*Aster vimineus*
Ludvigia alata	*Aster umbellatus*
Rhexia virginica	*Coreopsis tripteris*
Oxypolis rigidior	

In open places in the meadow the ground is covered by a varied growth of Cladonia (*C. furcata, C. pyxidata, C. verticillata, C. mitrula, C. cristatella, C.*

FIG. 36. The first step in the re-occupation of tilled Clermont silt loam: *Aristida gracilis* meadow. To the left, an old secondary oak forest; in the distance, an area of primary forest of the till plain.

subcariosa, and others). Mosses, especially *Polytrichum ohioense*, are common; locally Sphagnum is important.

The herbaceous meadow community of the white clay always contains an admixture of shrubs or is nearly supplanted by a shrub community. Here are found in greatest abundance, the "characteristic shrubs" of the till plain (except *Viburnum pubescens* var. *indianense*), as well as other shrub species:

Cephalanthus occidentalis	*Rosa setigera*
Cornus obliqua	*Rubus frondosus*
Cornus racemosa	*Rubus trivialis*
Corylus americana	*Salix discolor*
Hypericum prolificum	*Spiraea alba*
Ilex verticillata	*Spiraea tomentosa*
Pyrus melanocarpa	*Vitis labrusca*
Rosa carolina	

Locally, in the wettest places, Cephalanthus is dominant. The roses, *R. carolina* and *R. setigera*, frequently dominate large areas (Fig. 37). *Spiraea tomentosa* is, in many places, the most important shrub and may nearly supplant the other species.

Tree invasion of the mixed herbaceous meadow and of the shrub meadow of the white clay is similar. The trees of the initial stages of primary forest

are the important invaders, though in many places, particularly in the denser shrub meadows, little invasion is taking place.

Secondary Pin Oak Forest

Pin oak in pure or almost pure stand covers a large part of the area now in forest and is by far the most important type of secondary forest. Such stands vary in age from but a few years to 60 to 70 years (Fig. 37). Twenty years ago numerous young stands were springing up; today, few areas are returning to pin oak. This change is due to ditching, the effects of which have become much more pronounced in the last decade. In this respect, the Indiana area of Illinoian drift contrasts strongly with the Ohio area. There, young stands of pin oak or sweet gum are frequently seen. Less effort has been made there to utilize the land; roadside and field ditching is not as extensive and consequently the water table is higher. Thus conditions are still favorable for the invasion of the more hydrophytic trees of initial primary forest stages and unfavorable to the invasion of such intolerant tree species as sassafras.

Where secondary pin oak forms a closed stand it eliminates almost all the herb and shrub species of the meadows. A few sedges, an occasional straggly Ilex or rose, are all that remain of the earlier vegetation. Poison ivy is usually the dominant ground cover, forming a shrub layer 1 to 3 feet in height.

FIG. 37. Secondary sedge meadow invaded by wild roses (*Rosa setigera* and *Rosa carolina*). Secondary stand of pin oak about 60 years of age beyond.

Irregular invasion by pin oak, leaving small more or less open spots, allows the meadow and shrub species to persist. Such places are almost identical with the pin oak openings of primary areas, and in some places where surroundings furnish no evidence, cannot with certainty be distinguished from primary areas.

Crowded stands of pin oak become very tall. With dying off of all lower branches and a greatly elevated canopy more light is admitted and the understory becomes more varied. The secondary pin oak forest 60 to 70 years old is very similar to the pin oak consocies of the primary vegetation except that it occupies more extensive continuous areas (Fig. 38). Indications from understory are that it will be succeeded by a mixed forest similar to that which follows in primary succession.

Secondary Sweet Gum Forest

Locally, and only in the southern part of the area, sweet gum is the most important tree invader. Such stands are few, but are mentioned here, because in the Indiana area sweet gum shares with pin oak in importance in young and middle aged secondary forests.

Red Maple Groves

Red maple, or red maple and elm, with or without pin oak are the most important trees in secondary stands about the indefinable ravine heads of the

Fig. 38. Interior of old second growth stand of pin oak.

flats and in areas of Blanchester silt loam generally. Here, too, secondary succession appears closely to parallel the primary.

Secondary vegetation of the till plain is important, ecologically, because it is here that many of the most characteristic plants among the herbs and shrubs —those of high light requirements and hence of early developmental stages— find growth conditions most favorable. In these secondary areas they have become abundant and the vegetation is suggestive of probable early stages of the primary successions. Their behavior in the meadows and in the redeveloping forests and forest openings is of value in reconstructing the successions of these glacial plains.

V. THE SUCCESSIONS RECONSTRUCTED

The development of vegetation on the Illinoian till plains began soon after the recession of the Illinoian ice sheet. Changes in climate and in habitat since that time and the reactions of invading plants have directed a series of climatic successions with their included lesser successions. Probably at no time since the first invasion of plants onto the new glacial plain has a primary bare area been exposed. The vegetation of today is the result, not alone of factors operative today, but also of the influences effective during the earlier periods of vegetational occupancy of this area.

Originally the habitat was probably a very slightly undulating wet plain dotted with shallow pools. The soil was a calcareous drift. Into this, the pioneers of the post-Illinoian clisere invaded. Continued invasions, the migrations instituted by the changing climates of the Wisconsin glacial age, and changing environment directed a progression of vegetation. Gradual leaching of the upper part of the drift, soil formation, the action of organic acids in water-logged and poorly aerated soils, and the reactions of vegetation continued, producing the acid soils of 100 or even 50 years ago. Then man started his modification of the environment—by cutting, by plowing, and most of all by ditching and draining.

In the original vegetation, hydrophytes must have been more or less prominent. The hydrarch succession may have resembled the present secondary hydrarch succession. Or, bogs may have prevailed in deeper depressions, and bog successions and gradual filling of depressions followed. On flats, lichens and mosses were doubtless pioneers—a condition repeated locally in the secondary meadows. Herbaceous and shrub species, including at least a part of those which now make up the flora of secondary meadows, probably early became prominent. These post-glacial meadows doubtless contained a large number of species of more northern range than now exist here —for plants of the earlier migratory waves must have made up these communities. Some have persisted (Braun, 1928, and 1935a) ; other more southern species have entered, so that, while throughout the progress of the great

climatic successions in this area, there were meadow communities and still
are, the composition of these communities has continually been changed by
the influx of southern invaders.

The period of conifer dominance, amply demonstrated by Sears (1930)
on the youngest (Wisconsin) drift plains of Ohio, may never have been
effective here. No evidence of such occupancy remains, either on the Illinoian
till plain or along its margin.

Deciduous forest invasion, coincident with and dependent on the north-
ward migration of deciduous forest species, must have been attended by
the establishment of forests of the first invading species which found the
more or less hydrophytic conditions suitable. The number of such species is
limited. They must have been species which now range far northward. Some
of the poplars, probably *P. tremuloides, P. grandidentata* and others, willows,
and birch may have been among the first invaders. Occasional small groves
of aspen and popple are found on these flats, the aspen always associated with
some of the characteristic shrubs, the Spiraea, Ilex, etc.; these may be sec-
ondary invaders, or they may be relic species. *Salix discolor* is generally
scattered over the area. Of the present pioneer tree species, red maple and
white elm extend farther north than do the other species. This, together with
the greater mobility of their propagules, suggests that these species may have
preceded others of the present species. Such depressions which could, be-
cause of lesser depth, be first invaded by trees, would probably have been
occupied by these species. Hence the first reactions of forest vegetation upon
habitat would be of these species. Melin (1930) has demonstrated that dif-
ferent types of leaf litter decompose differently and yield different amounts of
nitrogen. The soil of those depressions first occupied would have been mod-
ified by the earliest invaders. Later entrants, as pin oak, would then have
found some areas already occupied and some soils modified by forest litter.
Present differences in soil types of depressions—the white Clermont silt loam
in some and the dark Blanchester silt loam in others—are due in part at least
to the influence of past vegetation. The latest entrant among the trees of
initial forest stages is sweet gum, a southern species still extending its range,
and at present general only in the southern half of the area.

In depressions in primary vegetation areas, succession has reached only the
first stages of tree invasion; such communities are still open, remnants of
meadow and shrub species remain, and the wide spacing of the trees permits
the continued entrance of pioneer tree species. In some, the large amount of
sweet gum in the understory points to a future greater importance of this
latest invader. The trees now in the open stands in depressions—as the pin
oaks of the open sedgy pin oak consocies—are apparently the first trees to
occupy the land on which they are growing. There is every indication that
the complete closing in of forest is an act of the last century or two, that

previous to that time openings acres in extent were not uncommon in the till plain forest. Later successional development is demonstrable by existing communities; earlier stages are theoretical, based only on evidences offered by relic species and remnants of communities, by soil differences, and by secondary successions.

The earlier progress of succession (through herb and shrub stages) was extremely slow; later, with forest invasion, succession moved more rapidly; and again, with the establishment of late successional stages (white oak-beech) the progress again becomes extremely slow. The extremely slow development at first, later acceleration, and finally, extreme retardation of rate of change exhibited by these till plain successions is typical of successions in which progress depends on reactions of the vegetation, rather than on external change (Cooper, 1926).

Set-backs in succession due to catastrophe of some sort have occurred from time to time. Fire has always been a factor modifying succession. In these wet areas it is not often effective, though a number of areas burned over in recent years have been seen. The harmful effect on shrubs and saplings because of their superficial roots is most pronounced and may in some instances have eliminated certain shrub species.

Windfalls opening up small areas in the forest favor the intolerant species and sometimes account for the presence of occasional pioneer species in communities of advanced successional rank.

Grazing of wood-lots is all too prevalent. Very few areas can be found which are not being grazed or do not bear evidence of having been grazed in the past. This has resulted in more or less complete destruction of the characteristic herbaceous and shrub species and in injury to or destruction of saplings. It also has tended to compact the soil, destroy the lighter humus layer and thus change the water relations (Auten, 1933). *Polygonum acre* is a good grazing indicator.

Drought is a factor of extreme importance. The shallow root systems of many of the species make them susceptible to drought. The persistence in the area of more or less hydrophytic relic species (Braun, 1928) precludes the possibility of protracted dry periods affecting the entire area. Droughts of shorter duration, such as experienced in 1930, affect local areas. The drought of 1930 was severe enough to dry many of the depressions normally the wettest and hence most poorly aerated sites. In many such places, beech, and in a few places, white oak, were killed. Roots in these situations are nearer the surface, hence suffered greatly by the drying out of depressions. Sunny openings are thus created in the forest in areas which are generally wet. Small pin oak, red maple, and sweet gum are thriving; herbaceous plants, more or less suppressed but still present, multiply rapidly and grow luxuriantly. In this way, depression communities successionally much younger than the sur-

rounding forest or communities out of accord with the surrounding **forest**
are produced. Some of the discrepancies in zonal arrangement and hence
apparent anomalies in succession may be due to the effects of occasional
droughts.

VI. SUMMARY

The forests of the Illinoian till plain of southwestern Ohio have been
shown to be ecologically distinct from the forests of surrounding dissected
areas. Occupying definite topographic sites favoring high soil water content
and the formation of acid soils, the forests are, in their earlier successional
stages, swamp forests. Only in the later stages are mesophytic conditions
reached, and even then the characteristic species of the mixed mesophytic for-
est of southwestern and southern Ohio are lacking. The vegetation is co-
extensive with the soil types on which it grows, soil types developed only in
southwestern Ohio and southeastern Indiana. Similar soils in the Illinoian
drift area of Illinois are drier and have developed under a drier climate; that
region is climatically unlike the Ohio area, and its vegetation not similar to
that of the Ohio area of Illinoian drift. Local areas of soils of similar color
and moisture on the Cumberland Plateau support vegetation somewhat similar
to that of the Ohio drift plains.

Climatic successions developing in the area have left their imprint on the
present vegetation. A close correlation between forest communities and
topography is evident and suggests the important rôle of soil water and soil
aeration as causal factors in community distribution. Topography, however,
changes but slowly, and the successions in progress are controlled largely by
the reactions of vegetation—shading, competition, and modification of soil.
The culmination of these successions leads to the establishment of a physio-
graphic climax of distinctly more northern aspect and composition than the
mixed mesophytic forest, the climatic climax of this geographic region.

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THE PARASITES OF SOME NORTH CAROLINA RODENTS

By

REINARD HARKEMA

Elon College
Elon College, N. C.

CONTENTS

THE PARASITES OF SOME NORTH CAROLINA RODENTS

INTRODUCTION

The parasites of rodents are of unusual interest. Probably because rodents are of small size and can be captured with comparative ease students of parasites have often examined them. Not only do many rodents carry infectious diseases but the damage they do to crops and forests results in losses of thousands of dollars annually. Rodents furnish very satisfactory material for the study of experimental parasitic infestations.

Fluctuations in the number of wild animals are of importance both in pure and applied ecology. These often result from epidemic diseases caused by animal parasites, bacteria, or fungi. Animal parasites usually are not fatal but may lessen the vitality so that infectious diseases are more serious.

PREVIOUS WORK

Wenyon (1926) has made a careful study of all protozoan parasites. Levine and Becker (1933) made a host and check list of the species of EIMERIA and this includes many rodent parasites.

Hall (1916) monographed the known nematodes from the orders Rodentia, Lagomorpha, and Hydracoidea. He described 34 species from North American rodents including 11 new species. Yorke and Maplestone (1926) included in their work on the "Nematode Parasites of Vertebrates" a list of all the known species of parasitic nematodes. The various trichostrongylids were treated by Nagaty (1932) who reduced the number of species found in rodents to five.

Several new species of tapeworms were reviewed by Stiles (1895). The cestode family Anoplocephalidae was reviewed thoroughly by Douthitt (1915) and Baer (1927). Meggitt (1924) monographed the cestodes of mammals and included a list of all known cestodes.

Trematodes are represented in very few species of North American rodents. The aquatic types such as the muskrat and the beaver are the only representatives which show an appreciable number of trematode species. These have been described by various authors. Barker (1915) in conjunction with various co-workers, and Price (1931) described the majority of the species from the muskrat.

The systematic classification of external parasites has been done by various specialists. Ferris has studied the Anoplura. The Acarina have been studied by Banks (1915) and Ewing (1922, 1925). The Ixodidae were monographed carefully by Nuttall, Warburton, and their associates (1908, 1911, 1915).

Baker (1904, 1905), Jordan and Rothschild have studied the fleas. Jordan
(1933) reduced the numerous American species of CERATOPHYLLUS by cre-
ating new genera for many of the species. Rocky Mountain spotted fever has
stimulated work upon the external parasites of mammals, especially in the
Bitter Root Valley, Montana. The fleas of the rodents were studied by Dunn
and Parker (1925) and *Dermacentor andersoni* Stiles was surveyed by Cooley
(1915, 1932), and Hooker, Bishopp, and Wood (1912).

The pathological and economic significance of special groups of rodents
has stimulated parasitological research on such animals. It is inadvisable to
discuss the results of such work. However, a cursory summary of the major
works is necessary. The helminth parasites of the rat were carefully sur-
veyed by Oldham (1932). The intestinal protozoa of the rat were studied by
Hegner (1929) and Kofoid, McNeil and Bonestell (1933). The presence of
Gongylonema neoplasticum (Fibiger and Ditlevsen 1914) and *Apophallus
donicum* (Skrjabin and Lindtrop 1919) in the rats of Washington is of sig-
nificant interest (Price and Chitwood, 1932). The external parasites of the
rat have been studied in various places. Fox and Sullivan (1925) have sum-
marized the subject very well.

The genus *Citellus* has been studied intensively. The protozoans were
covered very thoroughly by Becker (1926-1933) and co-authors and Henry
(1932). The helminths were studied by MacLeod (1933). The genera *Lepus*
and *Sylvilagus* have been studied rather intensively in various localities. A
summary of rabbit parasites and diseases was compiled by Schwartz and
Shook (1928, 1933). The parasites of the rabbits of Canada were surveyed
by Boughton (1932). The study of rabbits in Arizona was undertaken by
Vorhies and Taylor (1933) and those of Oklahoma by Ward (1934).
Weimer, Hedden and Cowdery (1934) made an investigation upon the hel-
minth parasites of rabbits in West Virginia.

MATERIALS AND METHODS

A total of 287 rodents including 41 cottontail rabbits, 53 gray squirrels, 54
white-footed mice, 84 house mice and 55 brown rats were examined for
parasites. The rabbits were collected from October, 1933 to August, 1934.
The other rodents were examined from May, 1934 to April, 1935. All of the
hosts were collected in Durham County and the majority of the forest dwellers
from the Duke Forest.

The only animals obtained alive throughout the period of observation
were the house mice, which were captured with box traps in various houses
and buildings in Durham, North Carolina. The rabbits and squirrels were
shot with a 0.12 gauge shotgun. The white-footed mice were captured with
the use of snap-traps. They were collected within 9 to 14 hours after the
baiting of the traps. Rats were captured alive during the summer months by

means of steel traps but these proved unsatisfactory during the fall and winter months when they were shot with a 0.22 rifle. The rats obtained during the summer months were collected from various meat and grocery establishments in Durham, N. C. Those shot were "dump" rats. When captured the animals were at once placed in tight cloth bags in order to prevent the escape of external parasites.

All of the animals with the exception of some of the squirrels, which were captured by a hired hunter, were removed to the laboratory and examined immediately for external parasites and protozoa. In some cases examination could not be completed immediately and the non-examined organs were placed in a cold room where the temperature remained at about 4° C.

In the laboratory hosts were removed from the cloth bags and combed carefully with a fine-tooth comb for external parasites. Fleas were killed with a chloroformed brush. Lice and mites were killed in hot 70 per cent alcohol. The cloth bag was then examined under a binocular microscope. All external parasites were preserved in 70 per cent alcohol and cleared in turpinol.

The host was skinned and blood and intestinal smears were made and examined for ten minutes each under high and low power objectives. Three fresh blood smears were obtained from the heart and liver. Three smears each were made from the stomach, duodenum, jejunum, ileum, caecum, colon, and rectum. The internal organs, the intercostal and diaphragm muscles were dissected under a binocular microscope and the parasites removed and washed in physiological salt solution. The muscles were also pressed between glass plates as an examination for trichina.

Protozoans were fixed in hot Bouin's fixative and stained in iron-alum haematoxylin. Nematodes were killed in 70 per cent alcohol and preserved in five parts of 70 per cent alcohol to one part of glycerin. Cestodes were allowed to die in tepid water to insure complete relaxation of the proglottids. Cestodes and trematodes were fixed and preserved in Conant's fixative of the following formula:

50 per cent alcohol	100.0 c.c.
Glacial acetic acid	2.5 c.c.
40 per cent formalin	6.5 c.c.

For microscopic examination and identification of the parasites cestodes were stained in Ehrlich's haematoxylin and trematodes in borax-carmine. They were mounted in damar. Nematodes were cleared in glycerin and examined.

The writer wishes to thank Dr. A. S. Pearse for the many helpful suggestions and criticisms given during the course of this work and the preparation of this manuscript. Thanks are also due to Dr. M. C. Hall for the use of the host catalogue of the Bureau of Animal Industry; to Dr. B. G. Chit-

HOSTS EXAMINED

After a preliminary survey of the rodents of North Carolina five were selected to study. These were species which varied in habits, size, and food and could be obtained in sufficient numbers to permit routine examinations throughout a year.

Sciurus carolinensis carolinensis Gmelin

The southern gray squirrel was selected for study as a comparatively large, arboreal mammal. The total length may be 250 cm.

Gray squirrels are active only during the day. They store up nuts, fruits, buds, seeds, and grains for times when food will be difficult to find. They do not hibernate although they may remain in the nest for long periods during inclement winter weather. They are strictly arboreal rodents and are not found away from forests.

The gray squirrel either builds a bulky nest of leaves and twigs in the crotch of a limb or else chooses a hollow in some rotted tree trunk. The young number from four to six and often two litters are raised a year.

Peromyscus leucopus leucopus (Rafinesque)

White-footed mice share with the meadow mice the distinction of being the commonest and most widely distributed of the North American small rodents. *Peromyscus leucopus leucopus* is a small rodent having a maximum length of 18 cm. with the tail less than half the total length. It frequents the cover of fallen logs, piles of rock, and other shelters such as are common in forests and brush lands. Occasionally it builds a nest in low bushes, or uses old nests made by birds. It is terrestrial, strictly nocturnal, and is active throughout the year. The food is almost strictly vegetarian. The number of young in a litter varies from three to seven but is usually four or five. There may be as many as four or five litters a year, hence young may be seen at almost any time.

Mus musculus musculus Linnaeus

This is the only species of the genus Mus which has established itself in North America. The maximum total length is 150 to 155 cm. While this mouse is more or less a "house" mouse it lives in open fields in many places. It is omnivorous but it is not as destructive as the rat.

Rattus norvegicus (Erxleben)

The brown, or Norway, rat has a maximum total length of 275 cm. It is perhaps the most thoroughly disliked of rodents. It frequently lives under filthy conditions, carries disease and is such a destructive creature that the hand of man has been set against it from time immemorial. The Norway rat is aggressive and so easily adapts itself to varying conditions that today it has a cosmopolitan distribution. It lives in great numbers in all large cities, on water-fronts, and is also widely spread over less inhabited districts, even frequenting fields and brushy areas where it finds favorable conditions.

Sylvilagus floridanus mallurus (Thomas)

The cottontail rabbit is a typical mammal of medium size and is widely distributed. In forested regions cottontail rabbits frequent only brushy areas among the trees, coming out to feed upon green vegetation in the late afternoon or early morning about the edges of fields or meadows. It is seldom seen in heavy stands of trees where there is no underbrush or an occasional glade. Cottontails are very prolific and in the warmer parts of their range young animals may be found during any month of the year. The production of several broods a year is general among representatives of this genus. The number of young in a litter varies from three to seven, with four as an average.

PARASITES WHICH INFESTED THE HOSTS EXAMINED

In this section the parasites found by the writer in each host are presented separately. The genus and species of the parasites, author and date of description, the average number of parasites per host, the percentage of hosts infested, and the part of the body which the parasite infests are given. Tables 1 to 5 present data by months for the various parasites.

SCIURUS CAROLINENSIS CAROLINENSIS Gmelin

CESTODA

1. Larval stage of *Taenia taeniaeformis* (Batsch 1786): 0.189, 1.89% ; liver.

NEMATODA

2. *Longistriata hassalli* (Price 1925): 77.5, 92.45% ; duodenum.

ARTHROPODA

ACARINA

3. *Atricholaelaps glasgowi* (Ewing 1925): 0.32, 13.2% ; on skin.
4. *Ixodes hexagonus* (Leach 1815): 0.075, 5.66% ; on skin.
5. *Trombicula* sp.: 6.35, 50.94% ; on skin.

ANOPLURA

6. *Hoploplcura sciuricola* (Ferris 1921) : 3.81, 32.64% ; on skin.
7. *Neohaematopinus sciurinus* (Mjöberg) : 28.75, 50.94% ; on skin.

SIPHONAPTERA

8. *Orchopeas wickhami* (Baker 1895) : 3.66, 50.94% ; on skin.

PEROMYSCUS LEUCOPUS LEUCOPUS (Rafinesque)

PROTOZOA

1. *Giardia microti* (Kofoid and Christiansen 1915) : 100% ; intestine.

TREMATODA

2. *Entosiphonus thompsoni* (Sinitsin 1931) : 0.11, 3.7% ; jejunum.

NEMATODA

3. Larval nematodes: 0.11, 1.85% ; encysted in the wall of the caecum.
4. *Rictularia coloradensis* (Hall 1916) : 0.203, 16.68% ; duodenum and jejunum.
5. *Syphacia peromysci* n. sp.: 4.94, 22.22% ; caecum.

ARTHROPODA
DIPTERA

6. Larva of *Cuterebra fontinella* (Clark) : 0.037, 1.85% ; in skin.

MUS MUSCULUS MUSCULUS Linnaeus

PROTOZOA

1. *Endamoeba muris* (Grassi 1879) : 13.09% ; small intestine.
2. *Trichomonas muris* (Grassi 1879) : 30.95% ; caecum.

CESTODA

3. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.35, 3.57; liver.
4. *Hymenolepis diminuta* (Rudolphi 1819) : 0.14, 1.19% ; small intestine.

NEMATODA

5. *Heterakis spumosa* (Schneider 1866) : 0.97, 10.71% ; caecum and rectum.

ARTHROPODA
ACARINA

6. *Echinolaelaps echidninus* (Berlese) : 0.04, 1.19% ; on skin.

SIPHONAPTERA

7. *Xenopsylla cheopis* (Rothschild 1903) : 0.15, 10.51% ; on skin.

RATTUS NORVEGICUS (Erxleben)

PROTOZOA

1. *Chilomastix bettencourti* (Fonseca 1913) : 5.4% ; intestine.
2. *Endamoeba muris* (Grassi 1879) : 1.8% ; small intestine.
3. *Trichomonas muris* (Grassi 1879) : 60% ; caecum.
4. *Trypanosoma lewisi* (Kent 1880) : 1.8% ; blood.

CESTODA

5. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.36, 12.72% ; liver.
6. *Hymenolepis diminuta* (Rudolphi 1819) : 0.29, 7.27% ; jejunum.

NEMATODA

7. Eggs of *Capillaria hepatica* (Bancroft 1893) : 2.6% ; liver.
8. *Heterakis spumosa* (Schneider 1866) : 0.52, 14.54% ; caecum and rectum.
9. *Nippostrongylus muris* (Yokogawa 1920) : 102.76, 78.18% ; duodenum and jejunum.
10. *Trichosomoides crassicauda* (Bellingham 1845) : 1.3, 47.2% ; urinary bladder.

ARTHROPODA
ACARINA

11. *Echinolaelaps echidninus* (Berlese) : 4.14, 27.27% ; on skin.

ANOPLURA

12. *Polyplax spinulosa* (Burmeister 1839) : 1.98, 7.27% ; on skin.

SIPHONAPTERA

13. *Xenopsylla cheopis* (Rothschild 1903) : 0.018, 1.8%.

The following parasites infested seven rats examined at Beaufort, N. C.

CESTODA

1. *Hymenolepis diminuta* (Rudolphi 1819) : 5.57, 71.42% ; jejunum.
2. *Hymenolepis nana* (Siebold 1852) : 3.85, 14.28% ; jejunum.
3. Larval stage of *Taenia taeniaeformis* (Batsch 1786) : 0.14, 14.28% ; liver.

NEMATODA

4. *Heterakis spumosa* (Schneider 1866) : 16.14, 85.71% ; caecum and rectum.
5. *Nippostrongylus muris* (Yokogawa 1920) : 28, 85.71% ; duodenum and jejunum.
6. *Trichosomoides crassicauda* (Bellingham 1845) : 4, 71.42% ; urinary bladder.

ARTHROPODA
ACARINA

7. *Echinolaelaps echidninus* (Berlese) : 3.42, 57.14% ; on skin.

SIPHONAPTERA

8. *Echidnophaga gallinacea* (Westwood 1875) : 1.14, 14.28% ; on skin.
9. *Xenopsylla cheopis* (Rothschild 1903) : 3.42, 57.14% ; on skin.

SYLVILAGUS FLORIDANUS MALLURUS (Thomas)

PROTOZOA

1. *Eimeria stiedae* (Lindemann 1865) : 36.58% ; white cysts in the liver.
2. *Enteromonas intestinalis* (Fonseca 1918) : 75.6% ; caecum.

TREMATODA

3. *Hasstilesia tricolor* (Stiles and Hassall 1894) : 1903.6, 41.46% ; small intestine.

CESTODA

4. Immature *Cittotaenia pectinata* (Goeze 1782) : 7.48, 78.07% ; duodenum and jejunum.
5. Mature *Cittotaenia pectinata* (Goeze 1782) : 1.78, 78.07% ; jejunum.
6. Larval stage of *Taenia pisiformis* (Bloch 1780) : 1.8, 31.7% ; attached to peritoneum or abdominal mesenteries.

NEMATODA

7. *Obeliscoides cuniculi* (Graybill 1923) : 19.63, 70.73% ; attached to the gastric mucosa.
8. *Trichostrongylus affinis* (Graybill 1924) : 48.14, 58.53% ; caecum and colon.
9. *Trichostrongylus calcaratus* (Ransom 1911) : 207.21, 80.48% ; duodenum and jejunum.

ARTHROPODA
ACARINA

10. *Haemaphysalis leporis-palustris* (Packard 1869) : 51.02, 100% ; on skin.
    Larvae : 12.9, 36.58%.
    Nymphs : 10.6, 48.78%.
    Adults : 27.4, 100%.

SIPHONAPTERA

11. *Cediopsylla simplex* (Baker 1895) : 7.7, 78.04% ; on skin.
12. *Odontopsyllus multispinosus* (Baker 1904) : 1.26, 17.97% ; on skin.

DIPTERA

13. Larva of *Cuterebra fontinella* (Clark) : 0.12, 7.07% ; in skin.

SUMMARY OF FINDINGS

PROTOZOA

There is a fundamental difference between protozoan infestations and helminthic infestations in that the protozoan parasites multiply in the body, resulting in a fluctuation in numbers, whereas in helminthic infestations the organisms do not multiply in the body and can be increased in number only by repeated reinfestation (Chandler, 1932).

Eight species of protozoa were found infesting the rodents examined by the writer. Squirrels were not regularly examined for protozoa but when examinations were made no protozoans were found. The white-footed mouse harbored one species; the house mouse, two species; the rat, four species; the rabbit, two species.

Giardia microti infested all of the white-footed mice examined by the writer. It was usually found in the duodenum but occasionally in the ileum and caecum.

Trichomonas muris was found infesting the caecum and occasionally the ileum of 60 per cent of the rats and in 30.95 per cent of the house mice examined by the writer. The presence of this protozoan is correlated with a pH of approximately 6.8 (Kofoid, McNeil, and Bonestell, 1933). The other protozoans found in rats were very rare. *Trypanosoma lewisi*, a blood protozoan, was found in one rat; *Chilomastix bettencourti*, in three rats; *Endamoeba muris* in one rat. The latter protozoan was more common in house mice, 13.05 per cent being infested.

Enteromonas intestinalis infested the caecum and colon of 75.6 per cent of the rabbits studied by the writer; *Eimeria stiedae* infested the liver of 36.58 per cent.

TREMATODES

Only two species of trematodes were found infesting the rodents examined by the writer. These parasites usually require a snail as an intermediate host and many species of trematodes are not expected in land animals in a region in which there is a paucity of fresh water.

Hasstilesia tricolor occasionally infested rabbits in enormous numbers at any season of the year. Seventeen (41.46 per cent) of the rabbits examined by the writer harbored this parasite, with an average of 1,903 parasites per host. The life history of this parasite is unknown but it probably encysts as the metacercaria upon vegetation. Infestation probably results from the ingestion of the encysted stage with the food. No correlation between the habitat of the host and the parasitic infestation can be made since the rabbit is a roaming animal.

Entosiphonus thompsoni, a trematode which is usually found in shrews, was found in two white-footed mice. The largest number of ENTOSIPHONUS

present in a single infestation was four. Krull (1934) also found this trema-
tode in the same host. The life-history of this species is unknown.

CESTODES

Five species of tapeworms infested the rodents examined. No cestodes
were found in Peromysous and, with the exception of one instance where a
host contained a larva of *Taenia taeniaeformis,* none was found in squirrels.
Three species were found in rats or mice and two infested rabbits.

Hymenolepis diminuta, a common tapeworm of the rat, was encountered
in only 7.27 per cent of the rats examined by the writer. This tapeworm
requires an intermediate insect host and the ingestion of the latter by a rat
for completion of its life cycle. Although only seven rats were examined at
Beaufort, *H. diminuta* was found in five of them, with an average of 5.5
worms per host.

Hymenolepis nana, the dwarf tapeworm, was found in one rat examined
at Beaufort, twenty-seven being present. This parasite infests rats and man
in various parts of the world. It is unique among cestodes in that it is
capable of completing its development from egg to adult in a single host.

The larval stage of *Taenia taeniaeformis,* the cat tapeworm, was found in
12.72 per cent of 35 rats and in 3.57 per cent of 84 house mice examined.
The largest number of parasites in an individual infestation was seven found
in a rat in February. This parasite occurred occasionally throughout the year
in rats but it was never abundant (Table 4). The squirrel harbored a single

TABLE 1

Sciurus carolinensis carolinensis

Showing occurrence of parasites during the months from September to May. The upper
figures in each instance indicates average number of parasites per host; the lower, the
percentage of hosts infested.

	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May
Number of hosts examined	7	10	8	5	10	6	3	3	1
Taenia taeniaeformis	0 0	0 0	0 0	0 0	0 0	0.16 16.66	0 0	0 0	0 0
Longistriata hassalli	110.33 95.71	102.6 100	101 87.77	13 60	106.9 100	62.33 100	19.33 100	46 100	16 100
Trombicula sp.	7.0 42.75	14.1 60	14.75 87.5	1.8 60	1.3 50	0.33 16.66	2.0 66.66	0 0	0 0
Atricholaelaps glasgowi	0.57 28.57	0.1 10	0 0	0 0	0.9 30	0 0	1 30	0 0	0 0
Ixodes hexagonus	0.14 14.2	0.2 10	0 0	0.2 20	0 0	0 0	0 0	0 0	0 0
Neohaematopinus sciurinus	2.7 14.44	2.6 50.0	6.5 87.5	80.2 100	101.3 90	2.16 16.66	0 0	0 0	0 0
Hoplopleura sciuricola	0.7 14.44	0 0	0.25 12.5	2.2 60.0	17.8 70.0	0 0	0 0	0 0	0 0
Orchopeas wickhami	0.72 28.57	0.3 20.0	1.0 62.5	13.6 60.0	3.1 60.0	9.5 66.66	7.0 100	1.33 33.3	1 100

specimen. There is only one other record of this parasite infesting squirrels of the United States (Dobrovsky and Harbough, 1934).

The only adult cestode found in 41 rabbits examined was *Cittotaenia pectinata*. CITTOTAENIA is the only genus of rabbit cestodes represented both in America and the Old World. Over 90 per cent of rabbits examined harbored this parasite; 78.7 per cent were infested with the adults and 65 per cent with immature forms. Young forms occurred most frequently in large numbers from individual rabbits collected in May, June and July. The average number of worms found in these months were 50, 7.8 and 8 respectively. In February there was an infestation of two of the five rabbits examined. Mature individuals of this cestode usually occurred singly or in pairs. On nine occasions 3, 4, or 5 worms were taken from rabbits during the warmer months. Infestation by CITTOTAENIA apparently takes places at all seasons of the year, with an increase during the spring months.

The larval stages of *Taenia pisiformis*, the dog tapeworm, were encountered in 31.7 per cent of the rabbits studied by the writer, with an average of 1.8 per host. The largest number of cysticerci found in an individual rabbit was 22. There appears to be no favorable time for infestation since sporadic occurrences of cysticerci were found throughout the year (Table 5).

NEMATODES

The rodents examined by the writer were infested with eleven species of nematodes. The squirrel harbored one species; white-footed mouse, two species; rat, five species; rabbit, three species. Squirrels and rabbits were infested only with strongyloids; white-footed mice, a spiruroid and an oxyuroid; rats, a strongyloid, an oxyuroid, a spiruroid and two trichuroids;

TABLE 2
Peromyscus leucopus leucopus
Showing occurrence of parasites during the months of the year, June, 1934 to April, 1935. The upper figure in each instance indicates average number of parasites per host; the lower, the percentage of hosts infested.

	Jan.	Feb.	Mar.	June	July	Aug.	Oct.	Nov.	Dec.
Number of hosts examined	5	7	8	5	7	6	5	5	6
Giardia microti	100	100	100	100	100	100	100	100	100
Entosiphonus thompsoni	0 / 0	0 / 0	0 / 0	0 / 0	0.85 / 28.57	0 / 0	0 / 0	0 / 0	0 / 0
Rictularia coloradensis	0 / 0	0 / 0	0 / 0	0.6 / 40.0	0.42 / 28.57	0.33 / 33.33	0 / 0	0.4 / 40.0	0.16 / 16.6
Syphacia peromysci	0 / 0	18.85 / 42.85	6.12 / 25.0	1.2 / 20.0	5.28 / 28.57	0 / 0	0 / 0	1.0 / 20.0	6.0 / 50.0
Larval nematode (Encysted)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	1.2 / 20.0	0 / 0
Cuterebra fontinella (larva)	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0 / 0	0.33 / 16.66

TABLE 3

Mus musculus musculus

Showing occurrence of parasites during the months of the year, June, 1934 to April, 1935. The upper figure in each instance indicates average number of parasites per host; the lower the percentage of hosts infested.

	Jan.	Feb.	Mar.	June	July	Aug.	Oct.	Nov.	Dec.
Number of hosts examined	7	8	5	7	16	33	5	7	6
Endamoeba muris	0	0	0	71.4	18.7	13.04	0	0	0
Trichomonas muris	57.42	50.0	40	28.5	43.7	13.04	20.0	42.8	33.3
Taenia taeniaeformis (larva)	0 0	0 0	0 0	0 0	0.06 6.2	0.08 8.6	0 0	0 0	0 0
Hymenolepis diminuta	0 0	0 0	0 0	1.71 14.2	0 0	0 0	0 0	0 0	0 0
Heterakis spumosa	0 0	0 0	0 0	0 0	0 0	0.95 4.3	1.4 20.0	7.0 85.7	0.16 16.6
Echinolaelaps echidninus	0.57 14.28	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0
Xenopsylla cheopis	0 0	0 0	0 0	0 0	0.43 31.2	0.26 17.3	0 0	0 0	0 0

house mice, the same oxyuroid as rats. All of the nematodes with the exception of *Trichosomoides crassicauda* infested the digestive system. The heligmosomid, *Longistriata hassalli,* was found in 92.45 per cent of the 53 squirrels examined, with an average of 77.5 per host. Table 1 shows this species to be very common throughout the period of study. No information concerning seasonal variation was obtained since no squirrels were examined during the summer months, but the worm probably is present throughout the year. The small number of parasites found in some of the hosts was influenced by the age of the host as young animals were usually not infested. Infestation by *Longistriata hassalli* is probably by skin penetration, the common method of infestation of other heligmosomids.

Rictularia coloradensis, a spiruroid, was encountered in 16.66 per cent of 54 white-footed mice examined by the writer. It usually occurred singly but occasionally two females were present. The males of RICTULARIA apparently do not remain long in the host, as none was found. Table 2 shows that no parasites were found during the first four months of the year. No examinations were made in May. The life-history of RICTULARIA is unknown.

Syphacia peromysci, n. sp., the oxyuroid of PEROMYSCUS, was found living free in the caecum. It was present in 22.22 per cent of the white-footed mice examined, with an average of 4.94 per host. It appears occasionally throughout the year (Table 2). The life-history of this species is unknown but probably simple as in other oxyuroids.

Heterakis spumosa, a rat and mouse nematode, is a non-pathogenic oxyuroid inhabiting the caecum and colon of rats and mice. It is rather

TABLE 4
Rattus norvegicus

Showing occurrence of parasites during the months of the year, May, 1934 to April, 1935. The upper figures in each instance indicates average number of parasites per host; the lower the percentage of hosts infested.

	Jan.	Feb.	Mar.	May	June	July	Aug.	Oct.	Nov.	Dec.
Number of hosts examined ..	6	5	7	5	5	5	4	8	5	4
Chilomastix bettencourti	0	0	0	20	40	0	0	0	0	0
Endamoeba muris	0	0	0	0	20	0	0	0	0	0
Trichomonas muris	50	60	66.66	80	60	60	75	62.5	60	50
Trypanosoma lewisi	16.6	0	0	0	0	0	0	0	0	0
Taenia taeniaeformis (larva)	0 0	1.8 40.0	0.14 14.25	0.4 20.0	1 20.0	0 0	0 0	0.37 25.0	0 0	0 0
Hymenolepis diminuta	0.16 16.66	0 0	0 0	0 0	0 0	2.8 40.0	0.25 25.0	0 0	0 0	0 0
Capillaria hepatica (eggs)	0	0	14.2	0	0	0	0	0	0	20
Heterakis spumosa	0.16 16.0	0 0	0 0	2.8 20.0	2.4 40.0	0.4 40.0	0 0	0 0	0 0	0 0
Nippostrongylus muris	122.83 83.3	44.6 100.0	71.57 62.5	6.2 40.0	146.4 80.0	71.4 100.0	208.25 100.0	247.37 87.5	39.2 80.0	17.5 25.0
Trichosomoides crassicauda	2.16 83.33	1.0 40.0	1.57 57.14	1.8 40.0	1.2 40.0	1.0 40.0	1.0 25.0	1.62 37.5	1.0 40.0	0.75 40.0
Echinolaelaps echidninus	7.16 50.0	1.2 60.0	7.57 28.57	9.2 40.0	0 0	0 0	0 0	0.36 12.5	12.83 33.3	0 0
Polyplax spinulosa	0 0	0 0	0.57 14.2	20.6 40.0	0 0	0 0	0 0	0.12 12.0	0 0	0 0
Xenopsylla cheopis	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0 0	0.25 25.0

common in other parts of the United States. It was rarely encountered during this survey. Eight of the 55 rats examined by the writer harbored these parasites, which were present during the summer months with the exception of a single individual found in January (Table 4). The eggs of *Heterakis spumosa* are viable for long periods of time under favorable conditions of temperature and moisture. They develop rapidly at summer temperatures. The life history is simple and the eggs become infective within fourteen days (Winfield, 1932). The mice on the other hand, harbored this parasite during the winter months (Table 3). The highest single infestation was 17 worms in a mouse examined in November when six of seven mice were infested. In general the rats of Beaufort appear to be more highly infested with this parasite than are those in Durham. Four of the seven rats examined showed comparatively high infestations—46, 29, 21 and 14 respectively.

The rat strongyloid, *Nippostrongylus muris*, was found in 78.18 per cent of the 55 rats examined by the writer. Large numbers were found in individual rats giving an average of 247.3 worms per host. The largest number

of worms found in an individual rat was 951. The infective larvae of *N. muris* enter rats by boring through the skin. When they are fed to rats only a small proportion are able to reach the intestine (Yokogawa, 1922). The infective larvae are carried to the lungs by the blood stream and pass through the respiratory system to the digestive system by way of the trachea.

The trichuroid, *Trichosomoides crassicauda*, is a parasite of the urinary tract of rats. It occurred in 47.2 per cent of the 55 rats studied by the writer, with an average of 1.3 worms per host. The parasites were present at any season of the year (Table 4). The largest number of worms present in a single infestation was 7. Infestation with this worm is by the ingestion of the eggs. The larvae are dispersed by means of the blood stream. Only those larvae which reach the urinary tract in their wanderings after having left the blood stream reach sexual maturity (Thomas, 1922).

TABLE 5
Sylvilagus floridanus mallurus

Showing occurrence of parasites during all months of the year, October, 1933 to September, 1934. The upper figures in each instance indicates average number of parasites per host; the lower, the percentage of hosts infested.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Oct.	Nov.	Dec.
No. of hosts examined	5	5	3	3	2	4	3	3	4	6	4
Eimeria stiedae	20	60	33.3	66.6	0	50	33.3	66.6	25.0	0	50.0
Enteromonas intestinalis	60	80	100	66.6	100	100	66.6	66.6	75.0	66.6	50.0
Hasstilesia tricolor	5152.2 80.0	2200.0 20.0	183.3 33.3	5696.0 66.6	0 0	5043.7 50.0	694.6 66.6	166.6 33.3	0 0	143.0 16.6	40.25 75.0
Cittotaenia pectinata Mature	1.2 80.0	1.4 80.0	1.0 66.6	0.66 33.3	3.0 100	3.25 75.0	1.66 66.6	1.66 66.6	3 75	1.0 83.3	1.75 100
C. pectinata Immature	6.4 60.0	9 40	3 66.6	3.6 100	50 100	7.8 100	8 66.6	1.33 66.6	3.0 25.0	1.16 33.3	3 75
Taenia pisiformis (larva)	1.6 40.0	0 0	2.66 66.6	2.33 33.3	3.5 50.0	6.25 50.0	0.33 33.3	0.33 33.3	3.75 50.0	0.5 16.6	0 0
Obeliscoides cuniculi	6.8 20.0	38.6 60.0	24.66 100.0	36.3 100.0	12.0 100.0	28.25 100.0	28.0 100.0	2.66 66.6	12.3 66.6	18.0 66.6	5.75 50.0
Trichostrongylus affinis	0 0	29.4 40.0	8.0 66.6	267.3 100.0	69.5 100.0	109.2 100.0	92.3 100.0	19.0 66.6	3.75 50.0	10.1 33.3	3.75 50.0
T. calcaratus	71.8 60.0	132.2 80.0	290.6 100.0	910.0 100.0	403.5 100.0	495.7 100.0	173.3 66.6	21.6 66.6	49.3 50.0	37.3 66.6	26.7 100.0
*Haemaphysalis leporis-palustris**	4.8 80.0	2.2 40.0	4.0 100.0	15.0 100.0	0 0	0 0	10.0 66.6	4.3 33.3	54.0 75.0	26.1 66.6	9.0 100.0
nymphs	4.4 80.0	1.6 40.0	6.6 66.6	7.0 100.0	48.5 100.0	5.5 50.0	5.3 66.6	16.6 100.0	31.5 75.0	5.6 50.0	4.75 75.0
adults	20.8 100.0	9.4 100.0	30.6 100.0	68.6 100.0	113.0 100.0	53.0 100.0	18.6 100.0	60.6 100.0	42.0 100.0	3.0 100.0	6.25 100.0
Cediopsylla simplex	5.2 80.0	12.1 100.0	28.6 100.0	13.6 100.0	4.5 100.0	9.7 100.0	1.5 50.0	4.0 66.6	0 0	2.8 66.6	2.2 75.0
Odontopsyllus multispinosus	0.2 20.0	0.6 20.0	12.6 100.0	3.3 66.6	0 0	0 0	0 0	0 0	0 0	0 0	0 0
*Cuterebra fontinella**	0.2 20.0	0 0	0 0	0 0	0 0	0.25 25.0	0 0	0 0	0.75 50.0	0 0	0 0

*Larvae

The trichuroid, *Capillaria hepatica,* was represented only by eggs in the liver of two rats. Infestation by this nematode is brought about by the ingestion of the eggs. Transmission is presumably through the eating of dead infested rats. If mature eggs are ingested hatching takes place in the small intestine and the newly liberated larvae, after penetrating the intestinal wall, reach the liver by way of the circulatory system according to Fülleborn (1924), but Nishigori (1925) and Asada (1925) believe that larvae pass through the intestinal wall into the abdominal cavity and then penetrate into the liver.

Only one specimen of the spiruroid, *Protospirura muris,* was found. This parasite requires an intermediate host such as a cockroach (Cram, 1926) during its life cycle.

The rabbit stomach worm, *Obeliscoides cuniculi,* was found in 70.73 per cent of the 41 rabbits examined by the writer, with an average of 19.6 per host. Examination of stomach walls of infested rabbits usually showed congestion of the gastric mucosa with numerous hemorrhages. The worms were usually free on the mucous membrane or embedded deep in the stomach wall. The rabbits examined by the writer show that infestation of OBELISCOIDES may occur throughout the year (Table 5). The largest number of worms found in an individual rabbit was 166. Infestation takes places through the mouth. There is no penetration of the skin by the infective larvae (Alicata, 1932).

The duodenum-jejunum nematode, *Trichostrongylus calcaratus,* occurred in 80.48 per cent of the rabbits examined by the writer, with an average of 207.2 per host. *Trichostrongylus affinis,* a nematode inhabiting the caecum and colon, was found in 58.53 per cent of the hosts examined, with an average of 48.1 per cent per host. Infestation of rabbits by species of TRICHO-STRONGYLUS may take place either through the skin or with the food. The latter is the more common mode of infestation (Sarles, 1932).

ARTHROPODS

Thirteen species of arthropods were found infesting the rodents studied by the writer. Squirrels carried six species; house mice, two species; rats, three species; rabbits, four species. No arthropods were found on PERO-MYSCUS, which were caught in snap traps, with the exception of two larvae of *Cuterebra fontinella* infesting one host.

Of the two mites found infesting the squirrels examined by the writer, an unidentified species of TROMBICULA larva, a chigger mite, was more common. It was found on 50.94 per cent of the 53 squirrels examined with an average of 6.35 per squirrel. The largest number of TROMBICULA found upon an individual squirrel was 103. This larval mite, the adults of which are free living, occurred during seven of the eight months of squirrel examination.

None were found in April when only three squirrels were examined for parasites. The largest average number of mites was found in October and November (Table 1). Undoubtedly these mites would prove to be more numerous during the summer months when TROMBICULA larvae are very numerous.

The mite, *Atricholaelaps glasgowi*, and the tick, *Ixodes hexagonus*, were uncommon, the former infesting only seven squirrels with an average of 0.32 per host; the latter, four specimens from three squirrels.

The louse, *Neohaematopinus sciurinus sciurinus*, was found upon 50.94 per cent of the squirrels, with an average of 26.7 per host. This louse was most prevalent during the month of December when an average number of 80.2 per host occurred. Lice were found whenever there was an appreciable number of hosts examined. *Hoplopleura sciuricola* showed an infestation of 22.64 per cent with an average of 3.81 per host. The largest number of HOPLOPLEURA found in a single infestation was 129 on a squirrel examined during January.

The flea, *Orchopeas wickhami*, occurred on 50.94 per cent of the squirrels examined, with an average of 3.66 per host. The largest number of fleas found was 57, found on a squirrel examined in December. Fleas were not prevalent during any of the months of the survey.

The rats examined by the writer harbored a mite, *Echinolaelaps echidninus*, a louse, *Polyplax spinulosa* and the tropical rat flea, *Xenopsylla cheopis*.

The mite was the most common, occurring on 27.27 per cent of the 55 rats examined, with an average of 14.14 per host. No mites were found during the summer months. The average number of parasites per monthly number of rats varied very little during the months it was present (Table 4).

The common rat louse was rarely collected (Table 4). Only 7.27 per cent of the rats were infested. The largest number of lice found was 53 in May. The average number per host was 1.98. Only one specimen of the tropical rat flea was collected. Fourteen *Xenopsylla cheopis* were collected from the 83 house mice examined. They were present only during July and August (Table 3). Low temperatures are harmful to the tropical rat flea (Bacot, 1914). The common rat flea, *Nosopsyllus fasciatus*, was not encountered during this survey. It appears that fleas are uncommon on Durham rats and mice. However at Beaufort, North Carolina, four of the six rats examined harbored fleas: *Xenopsylla cheopis* and *Echidnophaga gallinacea*, the tropical stick-tight flea. The average number of fleas per host was 3.42 for *Xenopsylla cheopis* and 1.14 for *Echidnophaga gallinacea*.

Two species of fleas and one species of tick were found infesting rabbits. *Haemaphysalis leporis-palustris*, the rabbit tick, was found upon all of the rabbits examined by the writer. This parasite requires three hosts upon which to feed in the larval, nymphal, and adult stages respectively. The

adults feed longer than the larvae or nymphs, therefore were found to be more numerous (Table 6).

Two species of fleas, *Cediopsylla simplex* and *Odontopsyllus multispinosus*. The former is the common rabbit flea of the Eastern United States and was found throughout the year. *Odontopsyllus multispinosus* is rather uncommon and was found only from February to May (Table 5). The greatest number occurred in March, an average of 12.6 per host. *Cediopsylla simplex* was more prevalent during February, March, and April (Table 5).

Four rabbits harbored the larval stages of a fly, *Cuterebra fontinella* (Table 5).

DISCUSSION

The preceding summary indicates that there is a predominance of internal parasites in the rabbits and rats, which are of larger size than the other rodents studied and therefore offer a more suitable habitat for parasites. Both are voracious feeders and thus permit greater infestation. Numerous rabbits and rats facilitate the dispersal of the parasites through faeces, thus enhancing the opportunity for infestation and reinfestation. A rat is omnivorous and has filthy habits which make infestation easy through the ingestion of eggs or larvae or by skin penetration. Pearse (1930) found that large, omnivorous, cursorial rodents usually are the most highly parasitized. The prevalence of *Hymenolepis diminuta*, which requires an intermediate host for completion of its life history, at Beaufort is probably due to the comparatively large number of fleas infesting the rats. The rats of Durham are not very heavily infested with fleas and show little infestation with this tapeworm (Table 4). Pearse (1930) states that mature tapeworms are common in mammals in open fields. The writer has observed a dominance of tapeworms in the rabbit, which lives in the field and forest.

The squirrel, although a comparatively large rodent, was infested with only one species of internal parasite, a strongyloid nematode. It is a comparatively clean arboreal animal. Its food is usually limited to fruits, nuts, seeds, buds and bark, thus apparently limiting infestation by parasites. The infestation by the single nematode undoubtedly takes place during short forays upon the ground. The squirrels showed high infestation of this nematode (Table 1) "probably because shade and moisture in forests are favorable for the development of the eggs and because when the hosts visit the ground they go again and again to situations which are favorable for infestation" (Pearse, 1930).

Small rodents such as house mice and Peromysci do not offer very favorable habitats for any large number of parasites. It is a recognized fact that small animals usually harbor few parasites. The parasites which occur in great numbers must necessarily be minute in size.

Squirrels carried more species of external parasites than any other rodent studied by the writer (Table 1). Squirrels have a permanent nest to which they return. They run about on the ground and may become infested in this way. However, infestation is easier in the nest which is suitable for breeding and metamorphosis of the parasites. Lice and TROMBICULA larvae showed specificity for squirrels and were only common on them. Lice were occasionally collected from rats. Adult mites were found on rats although they were uncommon. The rabbit apparently is an ideal host for a large number of ticks. It is of a comparatively large size and frequents shrubby areas which favors tick infestation (Pearse, 1930).

SEASONAL VARIATION

No seasonal variation was demonstrated in SCIURUS since no examinations of squirrels were made during the summer months. Seasonal variation is evident only in the parasites of the rats and rabbits. These were numerous and occurred throughout the year thus giving opportunity for comparison of the degrees of infestation. No seasonal variation for *Hasstilesia tricolor, Hymenolepis diminuta*, larval tapeworms, *Trichosomoides crassicauda* and *Heterakis spumosa* was demonstrated.

Figure 1 shows a dominance of CITTOTAENIA during the spring and summer months. High initial infestation was followed by a decrease in numbers. In Canada rabbits are said to develop an almost complete immunity to CITTO-TAENIA with a change in diet from green vegetation to bark during the winter (Boughton, 1932). There is apparently a similar reaction in the rabbits studied by the writer. As the cestodes grow some of them are lost until only one or two adult parasites remain during the winter months.

Figures 2 and 3 indicate an increase of *Trichostrongylus affinis* and *T. calcaratus* during the spring months, with a gradual decrease in the number of worms later. The high infestation apparently is followed by a host immunity response with the discharge of worms (Stoll, 1932). As many as 2,000 *T. calcaratus* were taken from individual rabbits by the writer. In laboratory animals a lethal dose is approximately 1,000 worms (Sarles, 1932a). The results obtained by the writer indicate that there is a host immunity response similar to that found by Stoll (1932) and Sarles (1932) after experimental infestations. The decrease in the number of worms during the winter months is undoubtedly influenced by the unfavorable lower temperature for the free-living larval stages (Stoll, 1932).

Variations in temperature apparently influenced the seasonal variation of *Obeliscoides cuniculi* and *Nippostrongylus muris* (Tables 4 and 5). No evidences of immunity reactions to these parasites have been demonstrated. The immunity reactions of white rats to *Nippostrongylus muris* (Yokogawa, 1922) apparently does not hold true for the brown rat (Chandler, 1931).
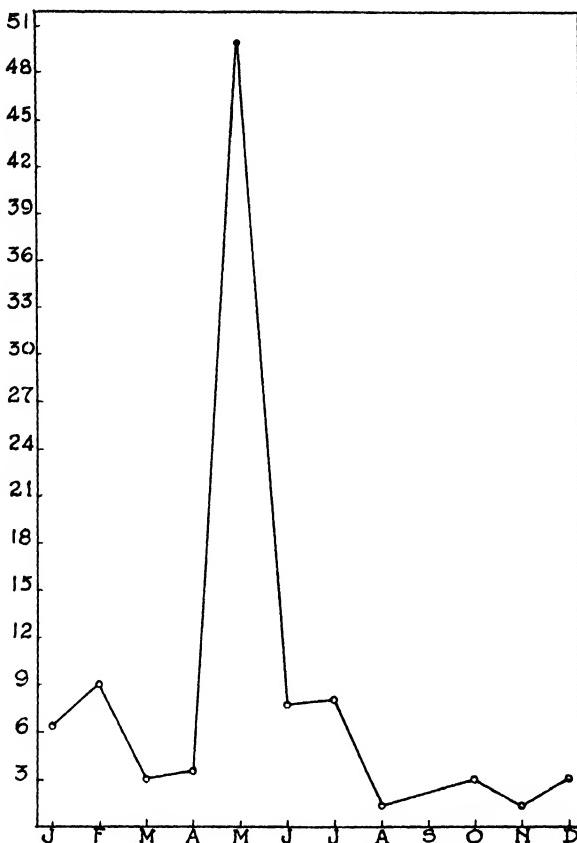
FIG. 1. Monthly variation in the average number of immature tapeworm, *Cittotaenia pectinata*, found in the cottontail rabbit, *Sylvilagus floridanus mallurus*, during a year.

Haemaphysalis leporis-palustris showed variations in the number of larvae, nymphs and adults appearing on the rabbits studied by the writer. The adults feed longer than the larvae or nymphs, therefore were found to be more numerous (Fig. 4). Hooker (1912) states from personal observation that large numbers of larvae and lesser numbers of nymphs when repleted abandon the host during the daytime. He regards this as an adaptation of the tick to the habits of their natural hosts, the hare and the rabbit. These remain during the day in their resting places and roam at night. The engorged ticks, dropping from the hosts in the resting places, undergo metamorphosis in a situation which favors their finding a host when they emerge and are ready to feed. In general the number of nymphs collected by the writer was greater than the number of larvae. The rabbits studied were collected during the day.

In Figure 4 an attempt is made to show the general succession of the
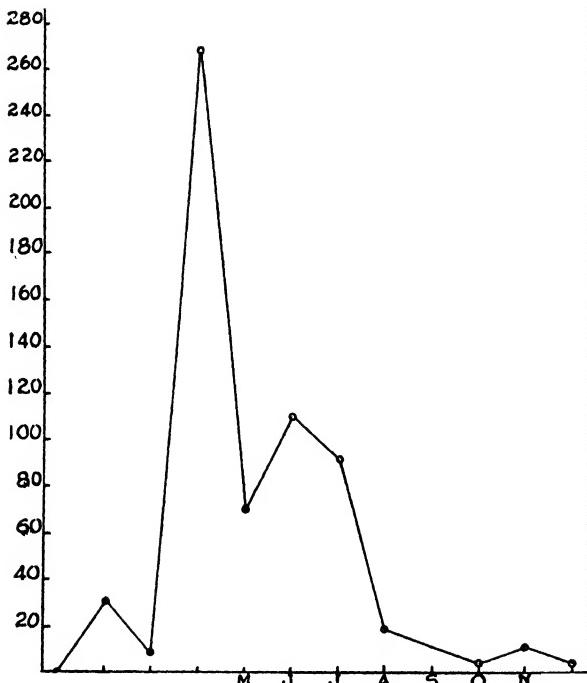
FIG. 2. Monthly variation in the average number of caecum nematode, *Trichostrongylus affinis*, found in the cottontail rabbit, *Sylvilagus floridanus mallurus*, during a year.

various stages of HAEMAPHYSALIS. The larvae are comparatively numerous during April, July and October, approximately 90 days separating each successive increase. The time required for the life-history of this tick at summer temperature is 87 days (Nuttall, Warburton, Cooper, and Robertson, 1915). The nymphs show periods of increase in numbers during May, August, and October. The periods of nymphal predominance follow those of the larvae, demonstrating a correlation between infestation and the life-history. There are also variations in the number of adults infesting the rabbits but there is no definite correlation between infestation and life-history since the feeding time for the host is greater than that of the larvae or nymphs. In general the adults are most abundant during the spring and late summer. The rate of metamorphosis is dependent upon the temperature. Figure 4 shows the correlation between monthly mean temperature and the average number of larvae, nymphs and adults. There is a decrease in the number of ticks with a decrease in temperature. A greater amount of time is necessary for metamorphosis at low temperatures and thus there are fewer parasites infesting the host. *Haemaphysalis leporis-palustris* apparently completes its life-history twice during the year.
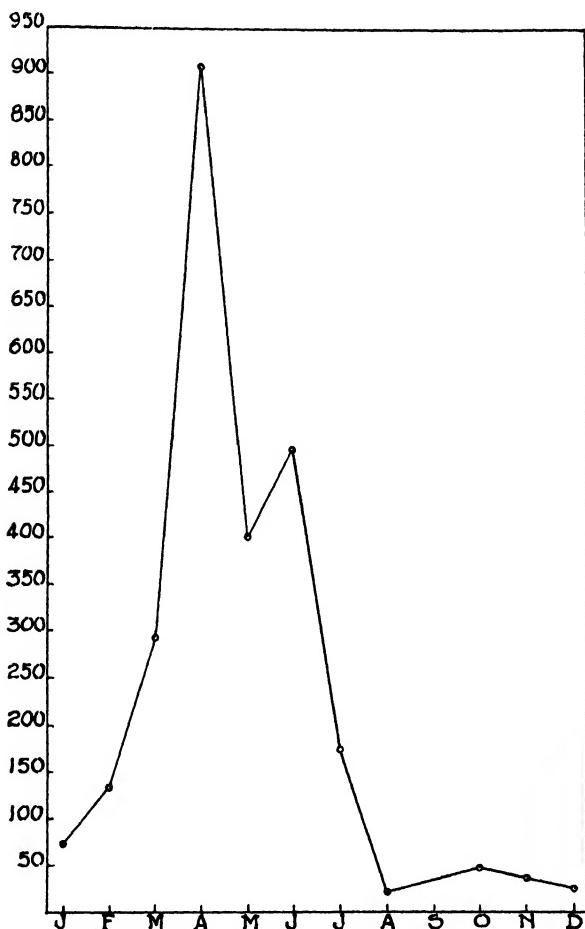
FIG. 3. Monthly variation in the average number of
duodenum nematode, *Trichostrongylus calcaratus*, found
in the cottontail rabbit, *Sylvilagus floridanus mallurus*,
during a year.

Table 5 shows the prevalence of *Cediopsylla simplex* and *Odontopsyllus multispinosus* during February, March and April. Many fleas, e.g. *Nosopsyllus fasciatus* increase in numbers during the colder parts of the year (Bacot, 1914). This apparently holds true for CEDIOPSYLLA and ODONTOPSYLLUS. Furthermore, rabbits remain in their resting places for longer periods of time when the temperature is low, thus permitting easier infestation by fleas.

CONCLUSIONS

Nearly all evidence indicates the desirability of elimination from valuable agricultural, range, and forest areas, of such species as the prairie dog, ground squirrel, and rabbit. The pocket gopher in a citrus orchard or an alfalfa field
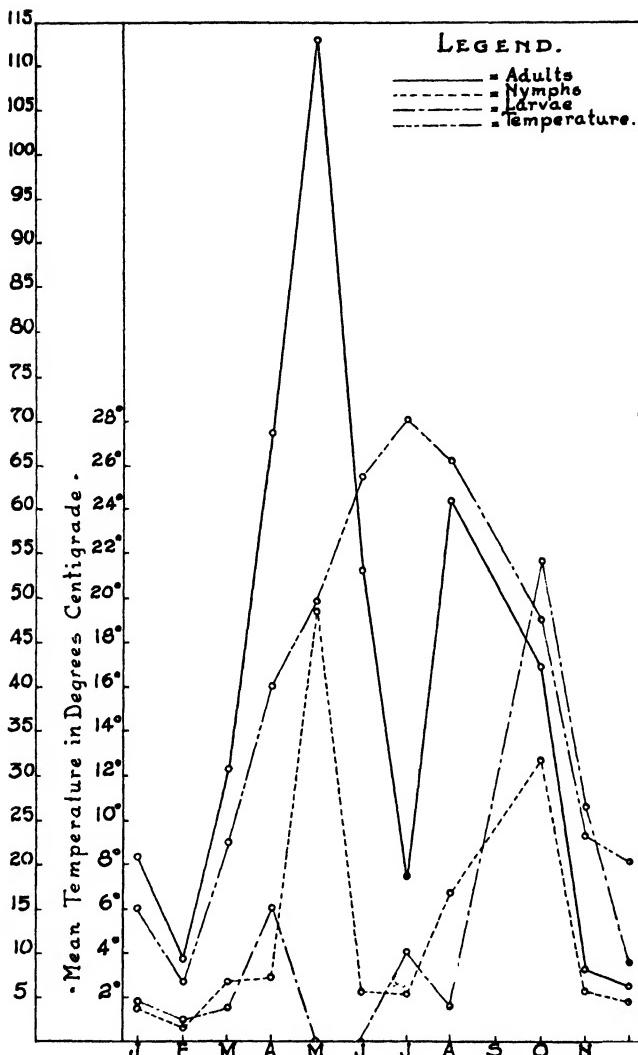
FIG. 4. Monthly variations in the average number of adults, nymphs, and larvae of the rabbit tick, *Haemaphysalis leporis-palustris,* during a year. The mean atmospheric temperature for the months in which observations were made is given.

is likewise undesirable. The California and Columbian ground squirrels must often be eliminated before profits can be made in cultivated areas. On the other hand, many rodents act as checks on insects. Some of the beneficial activities of rodents in the soil are: stirring up surface layers, increasing porosity; decreasing the size of particles; increasing aeration; increasing water percolation; helping to incorporate into the soil larger quantities of organic matter; depositing faeces and urine; depositing dead bodies. It must

be remembered that the injurious rodent effects are direct and easily observable, while beneficial rodent work is usually indirect and difficult to appreciate. The transmission of diseases by rats, ground squirrels, and rabbits is a menace to public health and control measures should be made with such rodents. The wholesale elimination of rodents has never been advocated, except for the obnoxious rat. "It is advisable to interfere with nature as much as necessary, but as little as possible" (Taylor, 1930).

A study of the writer's "List of Parasites of Rodents" makes one doubt the conception that a particular parasite is limited to a single host species and a single host may harbor but one species of a particular general group. Becker (1933) maintains that a particular parasite will develop in any host which provides satisfactory environmental conditions and mode of entrance and further that, "host-specificity becomes interpretable in terms of known physiological phenomena, and does not require any special interpretation involving a peculiar quality which species (host or parasite) possess that is separate and apart from what is observable in individuals."

Trematodes are uncommon in land rodents but in such aquatic types as the muskrat and beaver they are common. Trematodes are usually present in those rodents whose habitat are either in or near bodies of water. It is significant to note that the rodents of North Carolina, examined by the writer, showed only two species of trematodes and only one of these in any abundance.

It is a pertinent fact that the cestodes of the family Anoplocephalidae are well represented among herbivorous mammals. *Cittotaenia pectinata,* only adult cestode found in rabbits, is a member of this family. The life histories of the members of this family are unknown. Douthitt (1915) maintains that the type of soil determines infestation by anoplocephalids.

Omnivorous or insectivorous rodents usually harbor species of tapeworms belonging to families other than Anoplocephalidae. HYMENOLEPIS is a parasite of rodents and birds. These hosts are insect eaters and the birds more so than the rodents. There is a greater representation of Hymenolepididae in birds than in rodents.

Susceptibility, food, size and habits of the host, soil, and temperature undoubtedly influence the type of parasite and the degree of infestation. Seasonal periodicity may be influenced to some extent by the age of the host. Within the past 10 years there has been a widespread interest in observations or experiments dealing with the subject of resistance and susceptibility of helminthic infestations. Resistance to infestation or reinfestation by internal parasites has been shown to be correlated to some extent with the physiological status of the host. Rabbits show a tendency to lose their worms after initial infestation. Some of them show positive resistance to certain nematodes and show no infestation with them (Stoll, 1932). Furthermore, the

tendency to lose parasites may be associated with parasitic over-crowding, in the case of large tapeworms. The intestinal flora, and pH, undoubtedly influence the appearance and disappearance of internal parasites. Rabbits tend to lose their parasites in the winter months when food is scarce and the hosts resort to a bark diet (Boughton, 1932). An arboreal animal with a restricted herbivorous diet, for example, the squirrel, shows fewer internal parasites than a terrestrial animal which is omnivorous or has a non-restricted herbivorous diet, for example, rat and rabbit. In general the number of species of parasites is directly proportional to the size of the host. Temperature probably to some degree controls the infestation of hosts by fleas and ticks. It may influence the varying degrees of internal parasites during the various seasons, low temperatures being unfavorable to the free-living larvae.

SUMMARY

1. Scientific rodent control is advisable.
2. Two hundred eighty-seven rodents were examined for parasites: 53 gray squirrels, 54 white-footed mice, 84 house mice, 55 brown rats and 41 cottontail rabbits.
3. Eight species of protozoa were found infesting the rodents examined: white-footed mouse, 1; house mouse, 2; rat, 4; rabbit, 2.
4. Trematodes were uncommon in the rodents studied. One species was found in the white-footed mouse and one in the rabbit.
5. The rat, house mouse and rabbit were the only rodents found to harbor adult cestodes.
6. Eleven species of nematodes were found: squirrel, 1; white-footed mouse, 2; rat and house mouse, 5; rabbit, 3.
7. Seventeen species of arthropods infested the rodents examined: squirrel, 6; white-footed mouse, 1; rat, 4; house mouse, 2; rabbit, 4.
8. Smaller rodents harbor fewer parasites than do larger hosts.
9. Rodents having permanent nests are parasitized with more species of external parasites than are other rodents.
10. Arboreal habit lessens the possibility of internal parasites.
11. The type of food influences the character and degree of parasitism. Insectivorous rodents harbor cestodes requiring an insect as intermediate host. Herbivorous rodents harbor species of Anoplocephalidae, the life-histories of which are unknown.
12. Seasonal periodicity of parasites is influenced by temperature and change of diet. Susceptibility of hosts and immunity responses probably influence periodicity of infestation.
13. A list of parasites of North American rodents is presented in Appendix I.

14. The description of a new species of nematode from the white-footed mouse is presented in Appendix II.

APPENDIX I

A LIST OF PARASITES OF RODENTS

Here are listed the parasites reported from North American Rodentia and Lagomorpha. The parasites are arranged alphabetically under appropriate systematic groups and the hosts are listed in alphabetical order under them. Localities and bibliographic references for hosts are given whenever possible.

PROTOZOA

Babesia citelli Becker and Roudabush 1934
    Citellus tridecimlincatus t.; Iowa; Becker and Roudabush 1934, 524.
Balantidium sp.
    Dasyprocta aguti; Strong, Shattuk and Wheeler 1926, 130.
    Rattus norvegicus; Atchley 1935, 183.
Chilomastix bettencourti (Fonseca 1915)
    Rattus norevegicus; United States; Kofoid, McNeil and Bonestell 1933, 187.
C. magna Becker 1926
    Citellus tridecimlineatus texensis; Iowa; Becker 1926, 288.
Councilmania decumani Kofoid, Swezey and Kessel 1923
    Rattus norvegicus; Cosmopolitan; Kofoid, McNeil and Bonestell 1933, 187.
Eimeria beecheyi Henry 1932
    Otospermophilus grammurus g.; California; Henry 1932, 280.
E. bilamellata Henry 1932
    Callospermophilus chrysodeirus c.; California; Henry 1932, 282.
E. callospermophili Henry 1932
    Callospermophilus chrysodeirus c.; California; Henry 1932, 287.
E. citelli Kartchner and Becker 1930
    Citellus tridecimlineatus t.; Iowa; Kartchner and Becker 1930, 20.
E. cuniculi (Revolta 1878)
    Oryctolagus cuniculus domesticus; Levine and Becker 1933, 86.
E. cynomysis Andrews 1928
    Cynomys ludovicianus l.; Levine and Becker 1933, 86.
E. eubeckeri Hall and Knipling 1935
    Citellus franklinii; Iowa; Hall and Knipling 1935, 129.
E. falciformis (Eimer 1870)
    Mus musculus; Levine and Becker 1933, 86.

E. franklinii Hall and Knipling 1936
  Citellus franklinii; Iowa ; Hall and Knipling 1935, 129.

E. geomydis Skidmore 1928
  Geomys bursarius; Nebraska ; Skidmore 1929, 183.

E. irresidua Kessel and Jankiewicz 1931
  Oryctolagus cuniculus domesticus; Baltimore ; Kessel and Jankiewicz
  1931, 309

E. magna Pearard 1925
  Lepus californicus c.; California ; Levine and Becker 1933, 88, 97.
  Oryctolagus cuniculus domesticus; Iowa ; Becker 1933, 232, 234.
  Sylvilagus floridanus mearnsi; Iowa ; Becker 1933, 232, 234.

E. media Kessel and Jankiewicz 1931
  Lepus californicus c.; Levine and Becker 1933, 88, 97.
  Oryctolagus cuniculus domesticus; Levine and Becker 1933, 88, 97.

E. miyairii Becker and Hall 1931
  Rattus norvegicus; Iowa ; Becker and Hall 1931, 115.

E. monacis Fish 1930
  Marmota monax monax; District of Columbia ; Fish 1930, 99.

E. neotomae Henry 1932
  Neotoma fuscipes f.; California ; Henry 1932, 284.

E. nieschulzi Dieben 1924
  Rattus norvegicus; Levine and Becker 1933, 89.
  R. rattus rattus; Ibid.

E. ondatrae-zibethicae Martin 1930
  Ondatra zibethica z.; Nebraska ; Martin 1930, 273.

E. os Crouch and Becker 1931
  Marmota monax m.; Iowa ; Crouch and Becker 1931, 128.

E. perforans (Leuckart 1879).
  Lepus americanus a.; Canada ; Boughton 1932, 535.
  L. californicus c.; Levine and Becker 1933, 88, 97.
  Oryctolagus cuniculus domesticus; Levine and Becker 1933, 88, 97.

E. perforoides Crouch and Becker 1931
  Marmota monax m.; Iowa ; Crouch and Becker 1931, 128.

E. princeps (Labbe 1894)
  Oryctolagus cuniculus domesticus; Levine and Becker, 1933, 88, 97.

E. residua Henry 1932
  Neotoma fuscipes f.; California ; Henry 1932, 285.

E. schubergi (Labbe 1896)
  Mus musculus; Levine and Becker 1933, 97.

E. sciurorum Galli-Valerio 1922
  Sciurus niger rufiventer; Iowa ; Knipling and Becker 1935, 418.

E. separata Becker and Hall 1931

   Rattus norvegicus; Iowa ; Becker and Hall 1931, 131.

E. sprehni Yakimov 1934

   Castor canadensis c.; Canada ; Yakimov 1934, 294.

E. stiedae (Lindemann 1865)

   Lepus americanus a.; Canada ; Boughton 1932, 535.

   L. californicus c.; Levine and Becker 1933, 88, 97.

   Ondatra zibethica z.; Canada ; Law and Kennedy 1932, 30.

   Oryctolagus cuniculus domesticus; Cosmopolitan ; Schwartz and Shook 1933, 12.

   Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 84.

   S. f. mallurus; North Carolina ; this paper.

E. sp.

   Oryctolagus cuniculus domesticus; Canada ; Boughton 1932, 524.

   Sciurus griseus g.; Levine and Becker 1933, 92.

   Sciurus sp.; Ibid.

Endamoeba citelli Becker 1926

   Citellus tridecimlineatus texensis; Iowa ; Becker 1926, 444.

E. cuniculi Brug 1918

   Lepus californicus c.; Oklahoma ; Ward 1934, 84.

   Oryctolagus cuniculus domesticus; Wenyon 1926, 229.

   Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 84.

E. hystolytica (Schaudinn 1903)

   Rattus norvegicus; South Carolina ; Lynch 1915, 32.

E. muris (Grassi 1879).

   Mus musculus; North Carolina ; Harkema, this paper.

Enteromonas intestinalis Fonseca 1918

   Lepus californicus c.; Oklahoma ; Ward 1934, 84.

   Oryctolagus cuniculus domesticus; Wenyon 1926, 307.

   Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 84.

   S. f. mallurus; North Carolina ; Harkema, this paper.

Giardia beckeri Hegner 1926

   Citellus tridecimlineatus texensis; Iowa ; Hegner 1926, 203.

G. duodenalis Davaine 1875

   Lepus californicus c.; Oklahoma ; Ward 1934, 84.

   Oryctolagus cuniculus domesticus; Stiles and Boeck 1923, 180.

   Sylvilagus aquaticus a.; Oklahoma ; Ward 1934, 84.

   Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 84.

G. lamblia Stiles 1916

   Rattus norvegicus; California ; Kofoid, McNeil and Bonestell 1933, 187.

G. microti Kofoid and Christenson 1915

    Microtus californicus c.; California; Kofoid and Christenson 1915, 31.

    Peromyscus leucopus leucopus; North Carolina; Harkema, this paper.

    Peromyscus maniculatus gambeli; California; Kofoid and Christenson 1915, 31.

G. muris Grassi 1879

    Mus musculus; California; Kofoid and Christenson 1915, 31.

    Peromyscus maniculatus gambeli; California; Ibid.

    P. m. maniculatus; California; Stiles and Boeck 1923, 180.

    Rattus norvegicus; Missouri; Tsuchiya and Rector 1935, 426.

Haemogregarina citellicola (Wellman and Wherry 1910)

    Otospermophilus grammurus beecheyi; United States; Brumpt 1913, 101.

Hepatozoon muris (Balfour 1905)

    Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55.

    R. rattus rattus; United States; Brumpt 1913, 100.

Hexamitus marmotae Crouch 1934

    Marmota monax m.; Iowa; Crouch 1934, 513.

H. muris (Grassi 1881)

    Rattus norvegicus; California; Kofoid, McNeil and Bonestell 1933, 187.

H. pulcher Becker 1926

    Citellus tridecimlineatus texensis; Iowa; Becker 1926, 295.

Sarcocystis leporum Crawley 1914

    Sylvilagus floridanus mallurus; Maryland; Crawley 1914, 214.

S. muris Negri 1910

    Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55; Missouri; Tsuchiya and Rector 1935, 426.

Tetratrichomastix citelli Becker 1926

    Citellus tridecimlineatus texensis; Iowa; Becker 1926, 294.

Trichomonas cryptonucleata Crouch 1933

    Marmota monax m.; Iowa; Crouch 1933, 297.

T. digranula Crouch 1933

    Marmota monax m.; Iowa; Kentucky; Crouch 1933, 296.

T. intestinalis (Leuckart 1879)

    Rattus norvegicus; South Carolina; Lynch 1915, 22, 32.

T. marmotae Crouch 1933

    Marmota monax m.; Iowa; Kentucky; Crouch 1933, 296.

T. muris (Grassi 1879)

    Citellus tridecimlineatus texensis; Iowa; Becker 1926, 294.

    Mus musculus; United States; Stiles and Boeck 1923, 180.

    Peromyscus maniculatus gambeli; California; Kofoid and Christenson 1915, 31.

P. leucopus leucopus; Wenrich 1921, 120.

Rattus norvegicus; California; Kofoid, McNeil and Bonestell 1933, 187;
Missouri; Tsuchiya and Rector 1935, 427.

T. wenrichi Crouch 1933

Marmota monax m.; Kentucky; Crouch 1933, 296.

T. sp.

Citellus tridecimlineatus texensis; Iowa; Becker 1926, 296.

Trypanosoma brucei Plimmer and Bradford 1899 (experimental)

Peromyscus californicus c.; Michigan; Packanian 1934, 139.

P. eremicus anthonyii; Ibid.

P. e. eremicus; Ibid.

P. maniculatus artemisiae; Ibid.

P. m. bairdii; Ibid.

P. m. gambeli; Ibid.

P. m. osgoodi; Ibid.

P. m. ribidus; Ibid.

P. m. sonorensis; Ibid.

P. polionotus p.; Ibid.

P. truei gilberti; Ibid.

T. citelli Watson 1912

Citellus richardsonii; Canada; Watson and Hadwen 1912, 24.

T. cruzi Chagas 1909 (experimental)

Neotoma fuscipes annectens; California; Kofoid and Donat 1933, 258.

N. f. macrotus; California; Wood 1934, 497.

P. californicus c.; California; Kofoid and Donat 1933, 258.

P. eremicus fraterculus; California; Kofoid and Donat 1933, 258.

P. maniculatus gambeli; California; Wood 1934, 497.

P. truei giloerti; California; Wood 1934, 497.

Rattus norvegicus; California; Kofoid and Donat 1933, 258.

T. evotomys Hadwen 1912

Evotomys gapperi saturatus; Canada; Watson and Hadwen 1912, 25.

T. hippicum Darling 1910 (experimental)

Coendou laenatum; Panama; Clark and Dunn 1933, 275.

Dasyprocta punctata dariensis; Ibid.

T. hixsoni Becker and Roudabush 1934

Citellus franklini; Iowa; Becker and Roudabush 1934, 529.

T. iowensis Becker and Roudabush 1934

Citellus tridecimlineatus t.; Iowa; Becker and Roudabush 1934, 527.

T. leporis-sylvaticus Watson 1912

Sylvilagus floridanus mallurus; Canada; Watson and Hadwen 1912, 22.

T. lewisi (Kent 1882)

Neotoma fuscipes macrotus; California; Wood 1934, 497.

Rattus norvegicus; Cosmopolitan; Watson and Hadwen 1912, 24.

Rattus rattus r.; Wenyon 1926, 463.

T. microti Laveran and Pettit 1909

Microtus californicus c.; California; Wood 1934, 499.

M. pennsylvanicus; Nebraska; Coatney 1935, 456.

T. otospermophili Wellman and Wherry 1910

Otospermophilus grammurus beecheyi; California; Wellman and Wherry, 1910, 419.

T. peromysci Watson 1912

Peromyscus maniculatus m.; Canada; Watson and Hadwen 1912, 22.

P. m. nebracensis; Ibid.

T. sp.

Lepus californicus c.; Oklahoma; Ward 1934, 84.

Sylvilagus aquaticus a.; Ibid.

Sciurus sp.; Canada; Watson and Hadwen 1912, 24.

TREMATODA

Agomodistomum norvegicum Loewen 1934

Rattus norvegicus; Kansas; Loewen 1934, 250.

Alariae mustelae Bosma 1931

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Peromyscus leucopus noveboracensis; Michigan; Bosma 1934, 117.

Amphimerus speciosus (Stiles and Hassall 1898)

Rattus norvegicus; District of Columbia; Cram 1928, 72.

Apophallus donicum (Skrjabin and Lindtrop 1919)

Rattus norvegicus; District of Columbia; Price and Chitwood 1931, 55.

Ascotyle diminuta Stunkard and Haviland 1924

Rattus norvegicus; New York; Stunkard and Haviland 1924, 4.

Catatropis filamentis Barker 1915

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30; Nebraska; Harrah 1922, 55.

Cladorchis subtriquetrus Rudolphi 1814

Castor canadensis c.; Canada; Swales; 1933, 474, 476.

Echinochasmus schwartzi Price 1931

Ondatra zibethica z.; Maryland; Price 1931, 4.

Echinoparyphium contigerum Barker and Bastron 1915

Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Echinostomum armigerum Barker and Irvine 1915

Ondatra zibethica z.; Canada; Ibid.

E. callawayensis Barker and Noll 1915

Ondatra zibethica z.; Canada; Ibid.

E. coalitum Barker and Beaver 1915

    Ondatra zibethica z.; Canada; Ibid; Maryland; Krull 1935, 76.

E. revolutum (Froelich)

    Ondatra zibethica z.; Canada; Swales 1933, 474.

E. sp.

    Ondatra zibethica z.; Canada; Swales 1933, 480.

Entosiphonus thompsoni Sinitsin 1931

    Peromyscus leucopus leucopus; North Carolina; Harkema, this paper.

    P. l. noveboracensis; Maryland; Krull 1933, 49.

Fasciola hepatica Linnaeus

    Castor canadensis c.; Stiles 1895, 280.

    Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.

    Peromyscus leucopus noveboracensis; Maryland, Krull 1933, 98.

    Sylvilagus floridanus alacer; Louisiana; Dikmans 1930, 162.

    S. f. mallurus; Maryland; Krull 1933, 50.

Hasstilesia texensis Chandler 1929

    Lepus californicus texianus; Texas; Chandler 1929, 3.

    Sylvilagus floridanus alacer; Texas; Chandler 1929, 3.

H. tricolor (Stiles and Hassall 1891)

    Lepus americanus a.; Stiles and Hassall 1891, 160, 161.

    Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.

    Sylvilagus floridanus mallurus; Stiles and Hassall 1894, 160, 161.

    Sylvilagus sp.; Alabama; Noble and Smith 1932, 216.

Hemistomum craterum Barker and Noll 1915

    Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Heterechinostomum magnovatum Stunkard and Haviland 1924

    Rattus norvegicus; New York; Stunkard and Haviland 1924, 7.

Monostomum sp.

    Microtus pennsylvanicus p.; Stiles and Hassall 1894, 253.

Notocotyle hassalli McIntosh and McIntosh 1934

    Microtus pennsylvanicus p.; Maryland; McIntosh and McIntosh 1934, 36.

N. quinqueseriale Barker and Laughlin 1915

    Microtus pennsylvanicus p.; Maryland; Harrah 1922, 54.

    Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30; Washington; Harrah 1922, 54.

N. urbanensis (Cort 1914)

    Ondatra zibethica z.; Maryland; Harrah 1922, 51.

Nudacotyle novicia Barker 1916

    Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Paragonimus sp.

    Ondatra zibethica z.; Michigan; Ameel 1932, 382.

Paramonostomum echinum Harrah 1922.

   Ondatra zibethica z.; Colorado; Harrah 1922, 56.

P. pseudalveatum Price 1931

   Ondatra zibethica z.; Price 1931, 10.

Plagiorchis proximus Barker 1915

   Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Postharmostomum laruei McIntosh 1934

   Tamias striatus lysteri; Michigan; McIntosh 1934, 3.

Psilostomum ondatrae Price 1931

   Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

Renifer ellipticum Pratt 1903

   Castor canadensis c.; Philadelphia; Canavan 1934, 117.

Scaphiostomum pancreaticum McIntosh 1934

   Peromyscus gossypinus g.; Georgia; McIntosh 1935, 80.

   Tamias striatus lysteri; Michigan; McIntosh, 3.

Schistosomatium douthitti Price 1931

   Microtus pennsylvanicus p.; Price 1931, 691.

   Mus musculus; Price 1931, 691.

   Peromyscus maniculatus; Price 1931, 690.

S. pathlocopticum Tanabe 1923

   Rattus norvegicus; Massachusetts; Tanabe 1923, 197.

Stephanoproraoides lawi Price 1934

   Castor canadensis c.; Canada; Price 1934, 1.

Urotrema schillingeri Price 1931

   Ondatra zibethica z.; Maryland; Price 1931, 8.

Wardius zibethicus Barker and East 1915

   Ondatra zibethica z.; Law and Kennedy 1932, 30.

CESTODA

Andrya cuniculi (Blanchard 1891)

   Oryctolagus cuniculus domesticus; United States; Meggitt 1924, 206.

A. macrocephala Douthitt 1915

   Geomys bursarius; Minnesota; Douthitt 1915, 10.

A. primordialis Douthitt 1915

   Evotomys gapperi galei; United States; Baer 1927, 211.

   E. g. gapperi; United States; Baer 1927, 211.

   Microtus pennsylvanicus, p.; United States; Meggitt 1924, 19.

   Sciurus hudsonicus h.; Minnesota; Douthitt 1915, 5.

Anomataenia telescopica Barker 1915

   Ondatra zibethica z.; United States; Meggitt 1924, 56.

Caenotaenia pusilla (Goeze 1782)

    Rattus norvegicus; United States; Oldham 1931, 65.

    R. rattus rattus; United States; Oldham 1931, 65.

Cittotaenia ctenoides (Railliet 1890)

    Lepus californicus c.; Oklahoma; Ward 1934, 34.

    L. sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.

    Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.

    S. floridanus alacer; Oklahoma; Ward 1932, 84.

    S. f. mallurus; Pennsylvania; Smith 1908, 264.

C. pectinata (Goeze 1782)

    Erethizon dorsatum d.; United States; Baer 1927, 211.

    Lepus americanus a.; Canada; Boughton 1932.

    L. californicus c.; United States; Meggitt 1924, 26.

    L. c. melanotis; Nebraska; Douthitt 1915, 47.

    Oryctolagus cuniculus domesticus; Baer 1927, 213.

    Sylvilagus floridanus mallurus; North Carolina; Harkema, this paper.

    S. nuttalli nuttalli; United States; Meggitt 1924, 26.

    S. n. pinetis; United States; Baer 1927, 213.

    S. palustris p.; United States; Meggitt 1924, 29.

C. praecoquis Stiles 1895

    Geomys bursarius; United States; Baer 1927, 212.

C. sp.

    Geomys bursarius; Minnesota; Douthitt 1915, 62.

Cladotaenia sp.

    Cynomys bursarius; Scott 1931, 49.

Davainea sp.

    Geomys breviceps b.; Oklahoma; Douthitt 1915, 62.

Diandrya composita Darrah 1930

    Marmota flaviventris nosophora; Wyoming; Darrah 1930, 252.

Echinococcus granulosus (Batsch 1786)

    Oryctolagus cuniculus domesticus; Hall 1919.

Hymenolepis diminuta (Rudolphi 1819)

    Mus musculus; North Carolina; Harkema, this paper.

    Rattus norvegicus; District of Columbia; Stiles and Hassall 1894; California; McCoy 1909, 1370.

    R. rattus rattus; United States; Oldham 1930, 62.

    Sigmodon hispidus h.; United States; Meggitt 1924, 70.

    S. h. texianus; Smith 1908, 264.

H. evaginata Barker and Andrews 1915

    Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

H. fraterna (Stiles 1906)
> *Mus musculus;* Maryland; Shorb 1933, 91
> *Rattus norvegicus;* Maryland; Shorb 1933, 91.

H. nana (Siebold 1852)
> *Rattus norvegicus;* District of Columbia; Price and Chitwood 1931, 55;
> Missouri; Tsuchiya and Rector 1935, 427.

H. sp.
> *Geomys breviceps b.;* Oklahoma; Douthitt 1915, 62.
> *G. bursarius;* Illinois; Minnesota; Dakota; Douthitt 1915, 62.
> *G. personatus fallax;* Texas; Douthitt 1915, 62.
> *Ondatra zibethica z.;* Canada; Swales 1933, 480.

"Larval Tapeworm"
> *Cynomys leucurus;* Wyoming; Scott 1930, 115.
> *Sciurus carolinensis c.;* Maryland; Virginia; Schwartz 1928, 67.

Mesocestoides lineatus (Goeze 1782)
> *Mus musculus;* Hall 1919, 61.
> *Rattus norvegicus;* United States; Oldham 1931, 64.

Multiceps multiceps (Leske 1780) (larva)
> *Lepus americanus a.;* Canada; Boughton 1932, 213.
> *Lepus* sp.; United States; Meggitt 1924, 154.
> *Oryctolagus cuniculus domesticus;* United States; Meggitt 1924, 154.

M. packi Christenson 1929 (larva)
> *Lepus americanus a.;* Minnesota; Christenson 1929, 49.
> *L. californicus c.;* Oklahoma; Ward 1934, 84.
> *L. californicus c.;* Oklahoma; Ward 1934, 84.
> *L. campestris c.;* United States; Schulz 1931, 205.
> *Sylvilagus floridanus mearnsi;* United States; Schulz 1931, 206.

M. serialis (Gervais 1847) (larva)
> *Lepus americanus a.;* Canada; Boughton 1932, 213.
> *L. californicus c.;* United States; Hall 1919, 81
> *L. c. deserticola;* Ibid.
> *L. c. texianus;* Ibid.
> *L. c. wallawalla;* Ibid.
> *L. callotis;* Mexico; Meggitt 1924, 155.
> *L. campestris c.;* Meggitt 1924, 155.
> *Oryctolagus cuniculus domesticus;* Hall 1919, 81.
> *Rattus norvegicus;* United States; Oldham 1931, 65.
> *Sciurus carolinensis c.;* United States; Hall 1919, 81.
> *S. niger neglectus;* Ibid.
> *S. n. niger;* United States; Meggitt 1924, 155.
> *S. n. rufiventer;* Nebraska; Martin 1930, 804.

Sylvilagus floridanus mearnsi; United States; Bonnal, Joyeux and Bosch 1933, 1068.

S. palustris palustris; United States; Bonnal, Joyeux and Bosch 1933, 1068.

Oochoristica sp.

Geomys bursarius; Minnesota; Douthitt 1915, 62.

Paroniella retractilis (Stiles 1895)

Sylvilagus auduboni arizonae; Stiles 1895, 343.

Paranoplocephala infrequens (Douthitt 1915)

Evotomys sp.; North Dakota; Baer 1927, 212.

Geomys bursarius; Canada; Baer 1927, 212.

Microtus sp.; United States; Baer 1927, 212.

Prochoanotaenia spermophili MacLeod 1933

Citellus richardsonii; Canada; MacLeod 1933, 124.

C. tridecimlineatus t.; Canada; MacLeod 1933, 124.

Rallietina (Johnstonia) salmonis (Stiles 1895)

Lepus californicus melanotis; United States; Meggitt 1924, 49.

Sylvilagus floridanus mallurus; United States; Schulz 1931, 184, 185.

R. sp.

Geomys breviceps b.; Oklahoma; Meggitt 1924, 51.

Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 551.

Schizotaenia americana (Stiles 1895)

Erethizon dorsatum d.; United States; Baer 1927, 212.

E. epixanthum e., Ibid.

S. anoplocephaloides Douthitt 1915

Geomys breviceps b.; Oklahoma; Douthitt 1915, 35.

S. erethizontis (Beddard 1914)

Erethizon dorsatum d.; New York; Douthitt 1915, 33.

E. epixanthum e.; Alaska; Baer 1927, 116.

S. sigmodontis Chandler and Suttles 1922

Sigmodon hispidus h.; United State; Baer 1927, 211.

Sigmodon h. texianus; Texas; Chandler and Suttles 1922, 123.

Taenia hydatigena (Pallas 1766)(larva)

Mus musculus; District of Columbia; Stiles and Hassall 1894, 353.

Rattus norvegious; United States; Oldham 1931, 66.

R. rattus rattus; United States; Ibid.

Sciurus niger neglectus; Hall 1919, 81.

S. n. niger; Meggitt 1924, 160.   •

T. pisiformis (Bloch 1780) (larva)

Lepus americanus a.; Canada; Boughton 1932, 213.

L. californicus c.; Oklahoma; Ward 1934, 84.

L. c. wallawalla; California; Hall 1919, 81.

L. sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.

Mus musculus; Hall 1919, 81.

Oryctolagus cuniculus domesticus; Hall 1919, 81.

Rattus rattus r.; United States; Oldham 1931, 66.

Sylvilagus auduboni baileyi; Meggitt 1924, 164.

S. floridanus alacer; Oklahoma; Ward 1934, 84.

S. f. mallurus; Hall 1919, 82.

S. f. mearnsi; Hall 1919, 82.

S. nuttalli, n.; Meggitt 1924, 164.

S. n. pinetis; Hall 1919, 82.

S. palustris palustris; Hall 1919, 82.

T. portolae (Wellman and Wherry 1910) (larva)

    Otospermophilus grammurus g.; California; Meggitt 1924, 164.

Taenia taeniaeformis (Batsch 1786) (larva)

    Mus musculus; California; McCoy 1909, 1370; United States; Hall 1919, 81.

    Ondatra zibethica z.; Canada; Law and Kennedy 1932, 30.

    Rattus norvegicus; United States; Hall 1919, 81.

    Sciurus carolinensis c.; North Carolina; Harkema, this paper.

    S. n. rufiventer; Kansas; Dobrovsky and Harbough 1934, 67; Nebraska; Martin 1930, 804.

T. twitchelli Schwartz 1924 (larva)

    Erethizon epixanthum e.; Alaska; Schwartz 1924, 2.

T. sp.

    Erethizon dorsatum d.; District of Columbia; Stiles and Hassall 1894, 334.

    Sylvilagus floridanus mallurus; Ibid.

    S. palustris p.; Ibid.

Weinlandia citelli MacLeod 1933

    Citellus franklinii; Canada; MacLeod 1933, 122.

    C. richardsonii; Ibid.

    C. tridecimlineatus t.; Ibid.

NEMATODA

Ascaris laevis Leidy 1856

    Marmota monax m.; United States; Hall 1916, 41.

Capillaria gastrica (Baylis 1926)

    Rattus norvegicus; District of Columbia; Alicata and Lucker 1932, 311.

C. hepatica (Bancroft 1893)

    Castor canadensis c.; District of Columbia; Chitwood 1934, 10.

    Geomys bursarius; Philadelphia; Weidman 1917, 37.

    Ondatra zibethica z.; Canada; Swales 1933, 475.

    Rattus norvegicus; Hall 1916, 32.

R. rattus alexandrinus; Hall 1916, 32.

Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.

Thomomys fossor; Wyoming; Dikmans 1932, 84.

C. ransomia Barker and Noyes 1915

Ondatra zibethica z.; Nebraska; Hall 1916, 34.

C. sp.

Cynomys leucurus ludovicianus; Ratcliffe 1931, 37.

Castorstrongylus castoris; Chapin 1925

Castor canadensis c.; District of Columbia; Chapin 1925, 681; Philadelphia; Canavan 1931, 199.

Citellina marmotae Manter 1930

Marmota monax canadensis; Maine; Manter 1930, 29.

M. m. monax; New York; McClure 1934, 49, 51, 55.

Citellinema bifurcatum Hall 1916

Citellus elegans; Colorado; Hall 1916, 142.

C. monacis Manter 1930

Marmota monax canadensis; Maine; Manter 1930, 29.

C. quadrivittati (Hall 1916)

Eutamias quadrivittatus q.; Colorado; Schulz 1933, 77.

C. sleggsi Manter 1930

Citellus richardonii; Canada; Schulz 1933, 77.

Dermatoxys veligera (Rudolphi 1819)

Lepus alleni a.; Arizona; Vorhies and Taylor, 1933, 551.

L. californicus melanotis; United States; Hall 1916, 102.

Sylvilagus auduboni baileyi; United States; Hall 1916, 102.

S. nuttalli pinetis; Ibid.

Dipetalonema diacantha (Molin 1858)

Erethizon dorsatum d.; Minnesota; Jellison 1933, 43, 45.

Dirofilaria repens Railliet and Henry 1911

Erethizon dorsatum d.; Philadelphia; Canavan 1931, 223.

D. scapiceps (Leidy 1886)

Lepus campestris c.; United States; Schulz 1931, 136-137.

Sylvilagus floridanus alacer; United States; Ibid.

S. floridanus mallurus; United States; Hall 1916, 166.

S. palustris palustris; United States; Schulz 1931, 136-137.

D. spinosa Canavan 1929

Erethizon dorsatum d.; Minnesota; Jellison 1933, 43, 45.

D. subcutanea (Linstow 1899)

Erethizon dorsatum d.; Philadelphia; Canavan 1931, 221; Canada; Boulenger 1920, 492.

Filaria sp.

Castor canadensis c.; Michigan; Hall 1916, 188.

Filaria obtusa (Froelich 1791) *Protospirura muris* (Gmelin 1791)
  Rattus norvegicus; District of Columbia; Stiles and Hassall 1894, 339.
Gongylonema neoplasticum (Fibiger and Ditlevsen 1914)
  Rattus norvegicus; District of Columbia; Lucker 1931, 55.
Gongylonema sp.
  Castor canadensis c.; Michigan; Hall 1916, 198.
Graphidium strigosus (Dujardin 1845)
  Oryctolagus cuniculus domesticus; Schwartz and Shook 1933.
  Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.
  Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.
Heligmosomum vexillatum Hall 1916
  Rattus norvegicus; Colorado; Hall 1916, 157.
  Thomomys fossor; Colorado; Hall 1916, 157.
Heterakis spumosa Schneider 1866
  Mus musculus m.; Maryland; Winfield 1933, 177.
  Rattus norvegicus; United States; Hall 1916, 47.
  R. rattus rattus; Ibid.
Heteroxynema cucullatum Hall 1916
  Eutamias minimus oparius; Colorado; Hall 1916, 60.
Litosomoides carinii Vaz 1934
  Sigmodon hispidus h.; Mexico, Texas; Vaz 1934, 146.
L. patersoni Sandground 1934
  Sigmodon sp.; Sandground 1934, 596.
L. sigmodontis Chandler 1931
  Sigmodon hispidus h.; Texas; Chandler 1931, 6.
Longistriata adunca Chandler 1932
  Sigmodon hispidus h.; Texas; Chandler 1932, 25, 27.
L. carolinensis Dikmans 1935
  Peromyscus maniculatus nebracensis; Indiana; Dikmans 1935, 72-81.
L. dalrympei Dikmans 1935
  Ondatra zibethica z.; New Jersey, Indiana, Mississippi; Dikmans 1935, 72-81.
  Microtus pennsylvanicus p.; Ibid.
L. hassalli (Price 1928)
  Sciurus carolinensis c.; Maryland; Price 1928, 4.
L. musculi Dikmans 1935
  Mus musculus; Louisiana; Dikmans 1935, 72-81.
L. norvegicus Dikmans 1935
  Rattus sp.; Louisiana; Dikmans 1935, 72-81.
L. noviberiae Dikmans 1935
  Sylvilagus aquaticus littoralis; Louisiana; Dikmans 1935, 78.
  S. floridanus alacer; Louisiana; Ibid.

Microfilaria sp.

   Oryctolagus cuniculus domesticus; Canada; Harkin 1927, 113.

M. rosenaui McCoy 1911

   Otospermophilus grammurus beecheyi; California; Hall 1916, 189.

Micropleura sigmodoni Ochoterna and Caballero

   Sigmodon hispidus h.; Mexico; Ochoterna and Caballero 1932, 123-125.

Monodontus floridanus McIntosh 1935

   Sigmodon hispidus h.; Florida; McIntosh 1935, 29.   ˙

Nematode sp.

   Lepus californicus c.; Oklahoma; Ward 1934, 84.

Nematodirus leporis Chandler 1924

   Oryctolagus cuniculus domesticus; Texas; Chandler 1924, 2.

N. neotoma Hall 1916

   Neotoma cinerea rupicola; Colorado; Hall 1916, 138.

   N. desertorum; Colorado; Ibid.

   N. floridanus baileyi; United States; Travassos 1921, 30, 70, 115.

   N. mexicana fallax; United States; Hall 1916, 138.

   N. sp.; Hall 1916, 138.

N. triangularis Boughton 1932

   Lepus americanus a.; Canda; Boughton 1932, 532.

N. sp.

   L. alleni alleni; Arizona; Vorhies and Taylor 1933, 551.

Nematospira turgida Walton 1923

   Microtus pennsylvanicus p.; Illinois; Walton 1923, 61.

Nippostrongylus muris (Yokogawa 1920)

   Rattus norvegicus; Maryland; Yokogawa 1920, 29.

   R. rattus alexandrinus; Maryland; Graham 1934, 352.

Obeliscoides cuniculi (Grayvill 1923)

   Lepus californicus c.; Oklahoma; Ward 1934, 84.

   L. c. melanotis; New York; McClure 1932, 7, 14.

   L. sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.

   Oryctolagus cuniculus domesticus; Graybill 1923, 340.

   Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.

   S. floridanus alacer; Ibid.

   S. f. mallurus; Graybill 1924, 1.

Ollulanus tricuspis Leuckart 1865 (larva)

   Mus musculus; Hall 1916, 177.

Oxyuris tetraptera (Nitzsch 1821)

   Mus musculus; United States; Hall 1916, 89.

O. triradiata Hall 1916

   Ammospermophilus leucurus l.; United States; Hall 1916, 89

   Callospermophilus lateralis cinerascens; United States; Hall 1916, 89.

O. sp.
>   *Microtus pennsylvanicus p.;* United States; Stiles and Hassall 1894, 342.
>   *Pitymys pinetorum p.;* Maryland; Stiles and Hassall 1894, 342.

Passalurus ambigua (Rudolphi 1829)
>   *Lepus arcticus;* Hall 1916, 70.
>   *L. californicus c.;* Oklahoma; Ward 1934, 84.
>   *L.* sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.
>   *Marmota monax m.;* New York; Baker 1934, 48.
>   *Oryctolagus cuniculus domesticus;* United States; Hall 1916, 70.
>   *Sylvilagus floridanus alacer;* Oklahoma; Ward 1934, 84.
>   *S. f. mallurus;* Hall 1916, 70.

P. nonannulatus Skinker 1931
>   *Lepus americanus a.;* Canada; Skinker 1931, 5.
>   *Sylvilagus floridanus mallurus;* United States; Skinker 1931, 5.

Physaloptera spinicauda MacLeod 1933
>   *Citellus franklinii;* Canada; MacLeod 1933, 122.
>   *C. tridecimlineatus t.;* Canada; MacLeod 1933, 122.

Protospirura ascaroidea Hall 1916
>   *Geomys breviceps b.;* Oklahoma; Hall 1916, 120.
>   *Sigmodon hispidus texianus;* Oklahoma; Chandler and Suttles 1922, 123.

P. columbiana Cram 1926
>   *Rattus norvegicus;* District of Columbia; Cram 1926, 3.

P. muris (Gmelin 1790)
>   *Microtus pennsylvanicus p.;* Illinois; Walton 1924, 204.
>   *Mus musculus m.;* Hall 1916, 206; Illinois; Kudo 1924, 160.
>   *Rattus norvegicus;* United States; Hall 1916, 206.
>   *R. rattus alexandrinus;* United States; Hall 1916, 206.
>   *R. r. rattus; United States;* Hall 1916, 206.

Protostrongylus rufescens
>   *Sylvilagus nuttalli grangeri;* Scott & Honess 1932, 60.

Ransomus rodentorum Hall 1916
>   *Thomomys fossor;* Colorado; Hall 1916, 118.

Rictularia citelli MacLeod 1933
>   *Citellus franklinii;* Canada; MacLeod 1933, 122.
>   *C. tridecimlineatus t.;* Ibid.

R. coloradensis Hall 1916
>   *Eutamias quadrivittatus c.;* Colorado; Hall 1916, 175.
>   *Peromyscus leucopus l.;* North Carolina; Harkema, this paper.

Sincosta aberrans Roe 1929
>   "Wild Mouse"; New Jersey; Roe 1929, 3.

Spirura infundibuliformis MacLeod 1933
>   *Citellus richardsonii;* Canada; MacLeod 1933, 117.
>   *C. tridecimlineatus t.;* Canada; Ibid.

Strongyloides papillosus (Wedl 1856)
>   *Lepus americanus a.;* Canada; Boughton 1932, 530.
>   *Oryctolagus cuniculus domesticus;* United States; Ransöm 1911, 105.
>   *Rattus norvegicus;* United States; Hall 1916, 8; Canada; Boughton 1932, 530.

S. ratti Sandground 1925
>   *Rattus norvegicus;* Maryland; Sandground 1925, 71; Missouri; Tsuchiya and Rector 1935, 427.

Strongylus sp.
>   *Castor canadensis c.;* United States; Hall 1916, 109.

Synthetocaulus commutatus (Diesing 1851)
>   *Oryctolagus cuniculus domesticus;* Schwartz and Shook 1933, 22.

S. leporis Boughton 1932
>   *Lepus americanus a.;* Canada; Boughton 1932, 533-534.

S. rufescens (Leuckart 1865)
>   *Oryctolagus cuniculus domesticus;* Schwartz and Shook 1933.

Syphacia obvelata (Rudolphi 1802)
>   *Evotomys gapperi g.;* United States; Hall 1916, 82.
>   *Mus musculus m.;* Ibid.
>   *Neotoma mexicana fallax;* Ibid.
>   *Onychomys leucogaster l.;* Ibid.
>   *Peromyscus nasutus;* Ibid.
>   *Rattus norvegicus;* Ibid.
>   *R. rattus rattus;* Ibid.

Syphacia peromysci n. sp.
>   *Peromyscus leucopus leucopus;* North Carolina; Harkema, this paper.

S. thompsoni Price 1928
>   *Glaucomys volans v.;* Virginia; Price 1928, 2.

Travassosius americana Chapin 1925
>   *Castor canadensis c.;* District of Columbia; Chapin 1925, 679.

Trichinella spiralis (Owen 1835)
>   *Oryctolagus cuniculus domesticus;* United States; Stiles and Hassall 1894, 349.
>   *Rattus norvegicus;* United States; Hall 1916, 10.
>   *R. rattus rattus;* United States; Hall 1916, 10.

Trichosomoides crassicauda (Bellingham 1845)
>   *Rattus norvegicus;* United States; Oldham 1931, 78.
>   *R. rattus rattus;* United States; Oldham 1931, 78.

Trichostrongylus affinis Graybill 1924
>   *Sylvilagus floridanus mallurus;* Graybill 1924, 1.

T. calcaratus Ransom 1911
>   *Oryctolagus cuniculus domesticus;* Graybill 1924, 1.

Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 84.

S. f. mallurus; Maryland; Ransom 1911, 367.

T. colubriformis (Giles 1892)

Lepus californicus melanotis; Nebraska; Skidmore 1932, 800.

Sciurus aberti aberti; United States; Hall 1916.

Sciurus a. mimus; United States; Nagaty 1932, 470.

T. fiberius Barker and Noyes 1915

Ondatra zibethica z.; Nebraska; Hall 1916, 129.

T. retortaeformis (Zeder 1800)

Oryctolagus cuniculus domesticus; United States; Travassos 1921, 15, 41, 115.

T. sp.

Marmota monax m.; New York; McClure 1934, 49.

Trichuris fossor Hall 1916

Thomomys fossor; Colorado; Hall 1916, 23.

T. leporis (Froelich 1789)

Oryctolagus cuniculus domesticus; United States; Hall 1916, 25.

Lepus americanus a.; Canada; Boughton 1932, 539.

Lepus sp.; West Virginia; Weimer, Hedden and Cowdery 1934, 55.

Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 84.

S. floridanus f.; United States; Hall 1916, 25.

S. f. mallurus; United States; Hall 1916, 25.

T. opaca Barker and Noyes 1915

Ondatra zibethica z.; Nebraska; Hall 1916, 28.

Vestibulosetaria patersoni (Mazza 1923)

Sigmodon hispidus h.; Mexico; Vogel and Gabaldon 1932, 124.

Warrenius bifurcatus Hall 1916

Citellus richardonii; Canada; MacLeod 1933, 144.

W. quadrivittati Hall 1916

Eutamias quadrivittatus c.; Colorado; Hall 1916, 144.

Wellcomia evoluta (Linstow 1899)

Erethizon dorsatum d.; Philadelphia; Canavan 1931, 208.

E. epixanthum c.; Minnesota; Jellison 1933, 44.

Sylvilagus floridanus mearnsi; Kansas; Danheim 1924, 124.

ACANTHOCEPHALA

Acanthocephalid

Lepus americanus; Manitoba; Boughton 1932, 527, 539.

Moniliformis moniliformis (Bremser 1811)

Rattus norvegicus; Chandler 1921, 179.

R. rattus r.; Ibid.

Sciurus niger n.; Stiles and Hassall 1894e, 352.

M. spiradentatus MacLeod 1933
  Citellus tridecemlineatus t.; Canada; MacLeod 1933, 121.
M. sp.
  Neotoma sp.; Florida; Stiles 1932, 90.
  Sciurus niger n.; Texas; Chandler 1921, 179.

PENTASTOMIDA

Linguatula serrata (Froelich 1789)
  Oryctolagus cuniculus domesticus; Schwartz and Schook 1933.
Porocephalus sp.
  Erethizon dorsatum d.; Stiles and Hassall 1894, 354.

PARASITIC MITES

Atricholaelaps glasgowi (Ewing 1925)
  Sciurus carolinensis c.; North Carolina; Harkema, this paper.
Bdella cardinalis Banks
  Rattus norvegicus; New York; Fox and Sullivan 1925, 17.
Cyclolaelaps circularis Ewing 1932
  Peromyscus truei t.; Utah; Ewing 1933, 6.
Cytoleichus banksi Wellman and Wherry 1910
  Otospermophilus grammurus beecheyi; California; Wherry and Wellman
  1910, 421.
C. penrosei Weidman 1916
  Cynomys ludovicianus l.; Philadelphia; Weidman 1916, 82.
Dermanyssus evotomydis Ewing 1933
  Evotomys sp.; New York; Ewing 1933, 11, 13.
Echinolaelaps echidninus Berlese
  Mus musculus; Cosmopolitan; Banks 1910, 84.
  Rattus norvegicus; Ibid.
  R. rattus rattus; Ibid.
Euhaemogamasus americanus (Banks 1906)
  Peromyscus eremicus e.; Arizona; Banks 1906, 137.
E. microti Ewing 1925
  Microtus pennsylvanicus p.; New York; Ewing 1925, 142.
E. onychomydis Ewing 1933
  Onychomys sp.; Arizona; Ewing 1933, 4.
E. oregonensis Ewing 1933
  Dicrostonyx hudsonicus; Oregon; Ewing 1933, 5.
  Phenacomys albipes; Oregon; Ibid.
E. sanquineus (Ewing and Stover 1915)
  Rattus rattus rattus; Iowa; Ewing and Stover 1915, 111.
E. twitchelli (Ewing 1925)
  Evotomys dawsoni d.; Alaska; Ewing 1925, 143.

E. utahensis Ewing 1933
    Neotoma lepida l.; Utah; Ewing 1933, 41.

E. alaskensis (Ewing 1925)
    Microtus sp.; Alaska; Ewing 1925, 138.

Hannemania hirsuta Ewing 1931
    Perognathus californicus c.; California; Ewing 1931, 18.

Ichoronyssus carnifex (Koch)
    Mus sp.; Oregon; Ewing 1923, 15.

I. isabellensis (Oudemans)
    Mus sp.; District of Columbia; Ewing 1923, 16.

I. sternalis Ewing 1923
    Marmota monax m.; Plimmers Island; Ewing 1923, 14.

Laelaps hawaiiensis Ewing
    Rattus rattus r.; New York, New Orleans; Fox and Sullivan 1925, 1909.

L. hollisteri Ewing 1925
    Peromyscus californicus c.; California; Ewing 1925, 2.

L. multispinosus Banks
    Ondatra zibethica z.; Banks 1915, 84.

L. proheticus Banks
    Marmota monax m.; Banks 1915, 84.

Liponyssus bacoti (Hirst)
    Rattus norvegicus; District of Columbia, New York, Missouri, Texas; Ewing 1922, 19.

L. montanus Ewing 1922
    Citellus richardsoni; Montana, Canada; MacLeod 1933, 112.
    C. tridecimlineatus t.; Ibid.

L. occidentalis Ewing 1922
    Citellus richardsoni; Montana, Canada; MacLeod 1933, 112.
    C. tridecimlineatus t.; Ibid.

Listrophorus validus Banks
    Ondatra zibethica z.; Banks 1915, 127.

Myobia musculi Shrank
    Mus musculus m.; United States; Banks 1910, 84.

M. ratti Skidmore 1932
    Rattus norvegicus; Nebraska; Skidmore 1932, 172.

Neoschongastia brevipes Ewing 1931
    Peromyscus leucopus noveboracensis; Maryland; Ewing 1931, 16.

N. californicus (Ewing 1925)
    "Ground Squirrel"; California; Ewing 1931, 5.

N. peromysci (Ewing 1929)
    Peromyscus leucopus noveboracensis; Massachusetts; Ewing 1931, 5.

N. sciuricola (Ewing 1925)
    Sciurus hudsonicus richardsoni; Montana; Ewing 1931, 5.

Notoedres notoedres (Megnin)
  Rattus norvegicus; United States; Ewing 1929, 54.
  R. rattus rattus; United States; Ibid.
N. sp.
  Sciurus griseus g.; California; Bryand 1921, 128.
Psoroptes communis cuniculi (Delafond)
  Oryctolagus cuniculus domesticus; Schwartz and Shook 1933, 3.
  Lepus californicus c.; Oklahoma; Ward 1934, 83.
  Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 83.
  S. floridanus alacer; Oklahoma; Ibid.
Sarcoptes scabiei De Geer
  Rattus norvegicus; California; McCoy 1909, 1371.
Schizocarpus mingaudi Trouessart 1896
  Castor canadensis c.; Banks 1915, 127.
Tetragonyssus microti Ewing 1933
  Microtus californicus c.; California; Ewing 1933, 10.
  M. sp.; California; Ibid.
T. spiniger (Ewing and Stover 1915)
  Ondatra rivalicia; Louisiana; Svihla 1930, 287.
  O. zibethica z.; United States; Ewing 1923, 11.
Trombicula bisignalia Ewing 1929
  Microtus pennsylvanicus p.; Maine; Ewing 1929, 295.
  Peromyscus maniculatus abietorum; Maine; Ibid.
T. dentata Ewing 1925
  Sigmodon hispidus chiriquensis; Panama; Ewing 1925, 260.
T. dunni Ewing 1931
  Dasyprocta punctata nuchalis; Panama; Ewing 1931, 112.
T. harperi Ewing 1928
  Evotomys gapperi g.; New York; Ewing 1928, 79.
  Napaeozapus insignis i.; New York; Ibid.
  Sciurus hudsonicus h.; New York; Ibid.
T. irritans (Riley)
  Lepus californicus c.; Oklahoma; Ward 1934, 83.
  Sylvilagus aquaticus a.; Oklahoma; Ibid.
  S. floridanus alacer; Oklahoma; Ibid.
T. microti Ewing 1928
  Microtus pennsylvanicus modestus; Colorado; Ewing 1928, 80.
  M. richardsoni macropus; Wyoming; Ibid.
T. panamensis Ewing 1925
  Sigmodon hispidus chiriquensis; Panama; Ewing 1925, 260.
Trombicula sp.
  Sciurus carolinensis c.; North Carolina; Harkema, this paper.

IXODOIDEA

Amblyomma longirostre Koch

    Coendou rothschildi; Panama; Dunn 1923, 98.

A. maculatum Koch 1844

    Lepus californicus merriami; Texas; Bishopp 1912, 37.

A. parvus Aragao 1908

    Sigmodon hispidus chiriquensis; Panama; Dunn 1923, 99.

Dermacentor albipictus Packard

    Oryctolagus cuniculus domesticus; Bishopp and Wood 1913, 163.

D. andersoni Stiles (D. VENUSTUS Banks)

    Callospermophilus chrysodeirus c.; United States; Brumpt 1922, 758.

    C. lateralis cinerascens; Western United States; Hooker, Bishopp and Wood 1912, 166.

    Citellus columbianus c.; Montana; Cooley 1932, 47, 50.

    C. franklini; MacLeod 1933, 111.

    C. richardsonii; Canada, Montana; Ibid.

    C. tridecimlineatus t.; Canada; Ibid.

    Erethizon epixanthum e.; Jellison 1933, 43.

    Eutamias amoenus lutriventris; Montana; Cooley 1932, 32.

    E. umbrinus; Montana; Ibid.

    Lepus bairdii b.; Western United States; Hooker, Bishopp and Wood 1912, 166.

    L. campestris townsendi; United States; Brumpt 1922, 758.

    Marmota flaviventris f.; Western United States; Hooker, Bishopp and Wood 1912, 166.

    M. monax m.; Western United States; Ibid.

    Microtus pennsylvanicus modestus; Western United States; Ibid.

    M. nanus canescens; Western United States; Ibid.

    Neotoma cinerea c.; Western United States; Ibid.

    Ochotona princeps p.; Western United States; Ibid..

    Sciurus hudonicus richardsoni; Western United States; Ibid.

    Sylvilagus nuttalli n.; Western United States; Ibid.

    Thomomys fuscus f.; Western United States; Ibid.

D. electus Linnaeus

    Lepus callotis; Neumann 1901b, 365.

    L. sp.; Ibid.

D. occidentalis Neumann 1899

    Otospermophilus grammurus beecheyi; Wherry and Wellman 1909, 376.

D. perumapertus marginatus Banks

    Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 550.

    L. californicus; Arizona; Ibid.

    L. c. deserticola; Utah; Stanford 1934, 247.

    L. c. melanotis; Colorado; McCampbell 1926, 12.

D. variabilis (Say)

Microtus pennsylvanicus p.; Massachusetts; Parker, Philip and Jellison 1933, 349.

Peromyscus leucopus; Montana; Cooley 1932, 15; Massachusetts; Parker, Philip and Jellison 1933, 349.

Sciurus niger n.; Western United States; Hooker, Bishopp and Wood 1912, 191.

Sylvilagus aquaticus a.; Western United States; Ibid.

Haemaphysalis concinna Koch 1844

Marmota monax m.; Neumann 1901, 365.

H. flava Neumann 1897

Lepus sp.; Neumann 1901, 365.

H. leporis-palustris (Packard 1869)

Lepus americanus a.; Canada; Hewitt 1915, 230.

L. californicus c.; Oklahoma; Ward 1934, 83.

L. c. melanotis; Colorado; McCampbell 1926, 12.

L. sp.; United States; Neumann 1901, 365.

Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933, 27.

Sylvilagus aquaticus a.; Oklahoma; Ward 1934, 83.

S. floridanus alacer; Oklahoma; Ibid.

S. f. mallurus; North Carolina; this paper.

S. palustris p.; United States; Neumann 1901, 364.

Ixodes aequalis Banks 1909

Otospermophilus grammurus beecheyi; California; Wherry and Wellman 1909, 376.

I. angustus Neumann 1901

Lepus americanus a.; Canada; Hewitt 1915, 226.

Neotoma cinerea occidentalis; United States; Neumann 1901, 365.

Sciurus douglasii d.; Canada; Hadwen 1911, 37.

S. d. vancouverensis; Canada; Ibid.

I. a. woodi Bishopp 1911

Neotoma micropus m.; Texas; Nuttall 1916, 336.

I. banksi Bishopp 1911

Ondatra zibethica z.; Arkansas; Nuttall 1916, 337.

I. dentatus Marx 1899

Oryctolagus cuniculus domesticus; Neumann 1901, 324.

I. d. spinipalpis Hadwen and Nuttall 1915

Lepus americanus a.; Canada; Nuttall 1916, 304.

Sciurus douglasii; Canada; Ibid.

I. diversifossus Neumann 1899

Sylvilagus nuttalli n.; Montana; Bishopp 1912, 30.

S. n. grangeri; Utah; Stanford 1934, 247.

I. hexagonus Leach 1815
  Sylvilagus floridanus; Neumann 1901, 365.
I. hexagonus cookei (Packard 1869)
  Callospermosphilus chrysodeirus; San Francisco; Nuttall 1916, 328.
I. hexagonus inchoatus Neumann 1901
  Sciurus sp.; Neumann 1901, 365.
I. hexagonus (Leach) *longispinosus* Neumann 1901
  Marmota sp.; Neumann 1901, 365.
I. holocyclous Neumann 1899
  Sciurus sp.; Neumann 1901, 365.
I. kingi Bishopp 1911
  Citellus columbianus c.; Hooker, Bishopp, and Wood 1912, 82.
  Cynomys gunnisoni g.; Colorado; Burnett and McCampbell 1926, 7.
  Dipodomys ordii richardsoni; Hooker, Bishopp, and Wood 1912, 82.
  Sciurus hudsonicus richardsoni; Ibid.
  Thomomys talpoides clusius; Ibid.
  Ochotona princeps p.; Ibid.
I. loricatus Neumann 1899
  Neotoma cinerea occidentalis; Idaho; Neumann 1901, 172.
I. marxi Banks 1908
  Lepus californicus; Oklahoma; Ward 1934, 32.
I. pratti Banks 1908
  Thomomys sp.; California; Banks 1908, 28.
I. ricinus (Linnaeus)
  Lepus cuniculus; Neumann 1901, 364.
  Rattus norvegicus; Neumann 1901, 364.
  Sylvilagus floridanus mallurus; Neumann 1901, 365.
I. sculptus Neumann 1904
  Citellus tridecemlineatus t.; Iowa, Wyoming; Hixson 1932, 36, 42.
  Cynomys gunnisoni g.; Colorado; Burnett and McCampbell 1926, 7.
I. texanus Banks 1909
  Sciurus hudsonicus richardsoni; Bishopp 1912, 32.
I. sp.
  Lepus californicus deserticola; Utah; Stanford 1934, 247.
  Sciurus hudsonicus richardsoni; Montana; Birdseye 1912, 12.
Margaropus annulatus (Say)
  Rattus norvegicus; United States; Banks 1910.
Ornithodoros talaji Guern
  Rattus norvegicus; Dunn 1933, 477, 498.
  R. rattus; Ibid.

MALLOPHAGA

Eutrichophilus coendu Stobbe 1913
  Coendou mexicanum mexicanum; Mexico; Harrison 1916, 73.

E. setosus (Giebel)

    Erethizon dorsatum d.; Minnesota; Fenstermacher and Jellison 1932, 294.

Trichodectes geomydis Osborn

    Dipodomys merriami m.; Arizona; Kellogg and Ferris 1915, 73.

    Geomys bursarius; Ibid.

    C. cumberlandius; Ferris 1916, 99.

    Thomomys bottae b.; Kellogg and Ferris 1915, 73.

    T. bulbivorus; California; Paine 1912, 437.

    T. monticola m.; California; Ferris 1916, 99.

    T. sp.; California; Kellogg and Ferris 1915, 73.

ANOPLURA

Enderleinellus extremus Ferris 1919

    Sciurus colliae c.; Mexico; Ferris 1919.

    S. deppei d.; Mexico; Ibid.

    S. griseoflavus chiapensis; Mexico; Ibid.

    S. negligens; Mexico; Ibid.

    S. nelsoni; Mexico; Ibid.

    S. poleopis p.; Mexico; Ibid.

E. kelloggi Ferris 1916

    Sciurus goldmani; Mexico; Ferris 1919, 22.

    S. griseus nigripes; California; Ibid.

    S. griseus g.; California; Ibid.

E. longiceps Kellogg and Ferris 1915

    Sciurus aberti ferreus; Nebraska; Ferris 1919, 19.

    S. apache; Mexico; Ibid.

    S. arizonensis huachua; Ferris 1916, 148, 191.

    S. carolinensis c.; Mississippi; Ferris 1919, 19.

    S. kaibabensis; Arizona; Ibid.

    S. niger n.; Nebraska, Indiana; Ibid.

    S. n. rufiventer; Nebraska; Ibid.

    S. oculatus; Mexico; Ibid.

E. marmotae Ferris 1919

    Marmota monax rufescens; South Dakota; Ferris 1919, 47.

E. nitzschi Fahrenholz 1916

    Sciurus douglasii albolimbatus; California; Ferris 1919, 10.

    S. d. mollipilosus; California; Ibid.

    S. fremonti f.; Colorado; Ibid.

    S. hudsonicus petulans; Alaska; Ferris 1919, 9.

    S. h. vancouverensis; Alaska; Ferris 1919, 10.

    S. sp.; Ferris 1919, 10.

E. osborni Kellogg and Ferris 1915

    Citellus beldingi; Texas; Ferris 1919, 46.

Otospermophilus grammurus beecheyi; California; Kellogg and Ferris 1915, 71.

O. g. douglasii; California; Ferris 1919, 46.

O. g. fisheri; California; Ibid.

O. g. grammurus; Arizona; Ibid.

E. *suturalis* (Osborn 1891)

Ammospermophilus leucurus l.; Colorado; Ferris 1919, 43.

A. nelsoni nelsoni; California; Ibid.

Callospermophilus chrysodeirus c.; California; Ibid.

C. lateralis castanurus; Utah; Ibid.

Citellus beldingi; California; Ibid.

C. elegans; Colorado; Ibid.

C. franklinii; Iowa, North Dakota; Ibid.

C. mollis mollis; Nevada; Ibid.

C. oregonus; Nevada; Ferris 1916, 149, 187.

C. osgoodi; Alaska; Ferris 1919, 43.

C. townsendii; Washington; Ibid.

C. tridecimlineatus pallidus; Kansas; Ibid.

C. t. texensis; Oklahoma; Ibid.

C. t. tridecimlineatus; Iowa; Ibid.

Cynomys gunnisoni g.; Colorado; Ibid.

C. leucurus; Colorado, Wyoming; Ibid.

Otospermophilus grammurus g.; Arizona; Ibid.

Fahrenholzia microcephala Ferris 1922

Heteromys goldmani; Mexico; Ferris 1922, 161.

Liomys irroratus canus; Mexico; Ibid.

L. i. texensis; Mexico; Ibid.

L. pictus obscurus; Mexico; Ibid.

F. *pinnata* Kellogg and Ferris 1915

Dipodomys deserti d.; California; Kellogg and Ferris 1915, 73.

D. herrmanni californicus; California; Ibid.

D. merriami m.; California; Ferris 1916, 150.

D. ordii richardsoni; Oklahoma; Ibid.

D. ornatus; Mexico; Ferris 1922, 160.

D. philippsii; Mexico; Ibid.

D. sp.; Ferris 1916, 150, 193.

Perognathus parvus olivaceus; Nevada; Ferris 1922, 160.

F. *tribulosa* Ferris 1916

Perognathus californicus c.; California; Ferris 1916, 102, 1922, 163.

P. formosus; California; Ibid.

F. *t. reducta* Ferris 1922

Perognathus formosus; California; Ferris 1922, 166.

F. t. zacatecae Ferris 1922

    Perognathus hispidus zacatecae; Mexico; Ferris 1922, 166.

Haematopinoides squamosus Osborn 1891

    Geomys bursarius; Iowa; Ferris 1916, 180, 194.

Haemodipsus leporis

    Lepus californicus c.; Oklahoma; Ward 1934, 83.

H. lyriocephalus (Burmeister)

    Lepus arcticus a.; Ferris 1932, 330.

H. setoni Ewing 1924

    Lepus californicus c.; California; Ewing 1924, 550.

    L. c. melalnotis; Kansas; Ibid.

    L. campestris c.; Ferris 1932, 336.

H. ventricosus (Denny)

    Lepus californicus c.; California; Kellogg and Ferris 1915, 74.

    L. c. deserticola; Arizona; Ibid.

    L. campestris c.; Iowa; Ibid.

    Oryctolagus cuniculus domesticus; Ibid.

Hoplopleura acanthopus acanthopus (Burmeister 1839)

    Lagurus intermedius; Nevada; Ferris 1916, 154.

    Microtus californicus c.; California; Ferris 1921, 64.

    M. c. constrictus; California; Ibid.

    M. nanus nanus; Utah; Stanford 1934, 247.

    M. sp.; California; Iowa; Ferris 1921, 64.

    Neotoma cinerea c.; California; Ibid.

    Pitymys pinetorum p.; New York, Iowa; Ibid.

    Synaptomys sp.; Canada; Ibid.

H. erratica arboricola (Kellogg and Ferris 1915)

    Eutamias merriami pricei; California; Ferris 1921, 109.

    E. speciosus frater; California; Ibid.

    E. townsendii alleni; California; Ibid.

    E. t. ochrogenys; California; Ibid.

    E. sp.; California; Ibid.

    Tamias striatus striatus; California; Ibid.

H. e. erratica (Osborn 1896)

    Eutamias alpinus; California; Ferris 1921, 108.

    Tamias striatus striatus; California; Ibid.

H. hesperomydis (Osborn 1891)

    Mus musculus m.; California; Ferris 1916, 112.

    Onychomys leucogaster arcticeps; Colorado; Ibid.

    O. torridus longicaudus; California; Ferris 1921, 72.

    O. t. pulcher; California; Ferris 1916, 112.

    Oryzomys fulvestrus; Mexico; Ferris 1921, 72.

Peromyscus boylei b.; California; Ferris 1921, 71.

P. leucopus l.; Iowa; Ibid.

P. maniculatus gambeli; Utah, California; Ibid.

P. m. maniculatus; Iowa; Ibid.

P. m. rubidus; California; Ibid.

H. hirsuta Ferris 1916

Sigmodon hispidus eremicus; Arizona, California; Ferris 1916, 112; 1921, 117.

S. h. hispidus; North Carolina; Ibid.

S. h. texianus; Texas; Ibid.

S. ocrognathus; Mexico; Ibid.

Xenomys nelsoni nelsoni; Mexico; Ibid.

H. nesoryzomydis Ferris 1921

Zygodontomys seorsus; Panama; Ferris 1921, 90.

H. quadridentata (Neumann 1904)

Oryzomys fulvescens f.; Mexico; Ferris 1921, 88.

O. rostratus r.; Mexico; Ibid.

H. sciuricola Ferris 1921

Sciurus arizonensis huachua; Arizona; Ferris 1921, 110.

S. carolinensis c.; Florida, Mississippi; Ibid.

S. douglasii albolimbatus; California; Ibid.

S. d. douglasii; California; Ibid.

S. d. mollipilosus; California; Ibid.

S. griseus g.; California; Ibid.

S. hudsonicus h.; Alaska; Ibid.

S. h. vancouverensis; Alaska; Ibid.

S. kaibabensis; Arizona; Ibid.

S. sp.; Ibid.

H. trispinosa Kellogg and Ferris 1915

Glaucomys sabrinus lascivus; Oregon; Ferris 1921, 115.

G. volans volans; Maryland; Ibid.

Glaucomys sp.; California; Kellogg and Ferris 1915, 72.

Linognathoides inornatus Kellogg and Ferris 1915

Neotoma cinerea c.; California; Ferris 1923, 252.

Linognathoides montanus (Osborn)

Citellus armatus; Utah; Stanford 1934, 247.

C. beldingi; California; Ferris 1916, 99.

C. columbianus c.; Washington; Ferris 1916, 159.

C. mexicanus m.; Mexico; Ibid.

C. mollis m.; Utah; Stanford 1934, 247.

C. oregonus; Nevada; Ferris 1916, 99.

C. parryii kennicotti; Alaska; Ferris 1916, 159.

C. plesius ablusus; Alaska; Ferris 1916, 100.

C. sp.; Colorado; Ferris 1916, 159.

Cynomys leucurus l.; Colorado; Ferris 1916, 99.

Marmota flaviventris engelhardti; Utah; Stanford 1934, 24.

M. f. sierrae; Colorado, California; Ferris 1916, 159.

M. sp.; Oregon; Kellogg and Ferris 1915, 72.

Otospermophilus grammurus beecheyi; California; Ibid.

O. g. douglasii; California; Ferris 1916, 159.

O. g. grammurus; Arizona; Ferris 1916, 100; Utah; Stanford 1934, 247.

Sciurus niger neglectus; Ferris 1916, 100.

Linognathus piliferus (Burmeister)

Lepus washingtoni w.; California; Ewing 1924, 548.

Microphthirus uncinata (Ferris 1916)

Glaucomys sabrinus lascivus; California; Ferris 1919, 49.

Neohaematopinus inornatus (Kellogg and Ferris 1915)

Neotoma cinerea occidentalis; Ferris 1923, 252.

N. laeviusculus (Grube)

Callospermophilus lateralis castanurus; Utah; Ferris 1923, 264-265.

Citellus beldingi; California; Ibid.

C. columbianus c.; Washington; Ibid.

C. elegans; Colorado; Ibid.

C. mexicanus m.; Mexico; Ibid.

C. oregonus; Oregon; Ibid.

C. osgoodi; Alaska; Ibid.

C. parryii kennicottii; Alaska; Ibid.

C. plesius ablusus; Alaska; Ibid.

Cynomys leucurus; Colorado; Ibid.

Marmota flaviventris f.; Oregon; Ibid.

Otospermophilus grammurus beecheyi; Ibid.

O. g. beecheyi; California; Ibid.

O. g. grammurus; Arizona; Ibid.

N. marmotae Ferris 1923

Marmota flaviventris f.; California; Ferris 1923, 267.

M. sp.; Montana; Ibid.

N. pacificus; Kellogg and Ferris 1915

Eutamias alpinus; California; Ferris 1923, 249.

E. merriami pricei; California; Ibid.

E. speciosus frater; California; Ibid.

E. townsendii alleni; California; Ibid.

E. t. ocrogenys; California; Ibid.

E. t. sonomae; Ibid.

N. sciurinus sciurinus (Mjoberg)

    Hodomys alleni; Mexico; Ferris 1923, 244.

    Neotoma fuscipes streatori; California; Ibid.

    Sciurus aberti ferreus; Colorado; Ibid.

    S. apache; Mexico; Ibid.

    S. carolinensis c.; Mississippi; Ibid; North Carolina; Harkema, this paper.

    S. colliaei c.; Mexico; Ferris 1923, 244.

    S. deppei d.; Mexico; Ibid.

    S. douglasii albolimbatus; California; Ibid.

    S. douglasii d.; California; Ibid.

    S. d. mollipilosus; California; Ibid.

    S. griseus g.; California; Ibid.

    S. g. nigripes; California; Ibid.

    S. hudsonicus richardsoni; Montana; Ibid.

    S. nelsoni n.; Mexico; Ibid.

    S. niger neglectus; California; Ibid.

    S. n. rufiventer; Iowa, Indiana, Nebraska; Ibid.

    S. oculatus c.; Mexico; Ibid.

    S. poliopus p.; Mexico; Ibid.

N. sciurinus griseicolus Ferris 1923

    Sciurus griseus g.; California; Ferris 1923, 248.

N. sciuropteri Ferris 1916

    Glaucomys sabrinus lascivus; California; Ferris 1916, 170.

    G. volans v.; Iowa; Ibid.

    G. sp.; California, Ferris 1923, 241.

N. sp.

    Glaucomys volans v.; North America; Enderlein 1904, 143.

Philandesia foxi Ewing

    Marmota flaviventris; Washington; Ewing 1927, 87.

    Rattus norvegicus; New York City; Ewing 1927, 87.

Polyplax alaskensis Ewing 1927

    Microtus sp.; Alaska; Ewing 1927, 119.

P. auricularis Kellog and Ferris 1915

    Peromyscus maniculatus gambeli; Ferris 1916, 172.

    P. m. rubidus; Ferris 1916, 155.

    P. sitkensis prevostensis; Alaska; Ferris 1916a, 99, 172.

    P. truei t.; Utah; Stanford 1934, 247.

P. auricularis Kellog and Ferris 1915

    Neotomodon alstoni; Mexico; Ferris 1923, 219.

    Onychomys leucogaster articeps; Colorado; Ferris 1916, 172, 197.

    O. torridus pulcher; Colorado; Ibid.

    Reithrodentomys mexicanus m.; Mexico; Ferris 1923, 219.

P. spinulosa (Burmeister)
   Lagurus intermedius; Nevada; Ferris 1916a, 99.
   Microtus californicus c.; California; Ferris 1916, 176.
   M. sp.; California; Ferris 1923, 187, 188.
   Phenacomys longicaudus; California; Ferris 1916, 176.
   Rattus norvegicus; Ferris 1916, 176.
   R. rattus alexandrinus; United States; Ibid.
   R. r. r.; Panama, United States; Ibid.
   Synaptomys borealis; Canada; Ferris 1923, 128.

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Amphipsylla pollionis (Rothschild 1905)
   Evotomys gapperi saturatus; Canada; Jordan and Rothschild 1913, 406.
   Microtus drummondi d.; Canada; Ibid.
Anomiopsylla nudatus Baker 1898
   Neotoma albigula a.; Arizona; Baker 1904, 426, 452.
   Rattus sp.; California; Fox 1925, 217.
Atyphloceras bishopi Jordan 1933
   Microtus pennsylvanicus p.; New York; Jordan 1933a, 65.
A. felix Jordan and Rothschild 1915
   Mus sp.; Arizona; Jordan and Rothschild 1915, 60.
   Peromyscus truei t.; New York; Jordan 1933, 69.
Carteretta carteri Fox 1927
   Neotoma fuscipes f.; California; Fox 1927, 210.
Catallagia charlottensis (Baker 1898)
   Eutamias amoenus luteiventris; Montana; Dunn and Parker 1923, 2775.
   Lepus bairdii b.; Montana; Ibid.
   Peromyscus maniculatus artemisae; Montana; Ibid.
   P. m. macrochirus; Canada; Rothschild 1915, 43.
C. decipiens Rothschild 1915
   Evotomys gapperi saturatus; Canada; Rothschild 1915, 43.
   Neotoma cinerea c.; Canada; Ibid.
Cediopsylla inaequalis (Baker 1895)
   Citellus columbianus c.; Montana; Dunn and Parker 1923, 2775.
   Lepus bairdii b.; Montana; Ibid.
   Lepus californicus melanotis; Colorado; McCampbell 1926, 12.
   L. campestris c.; Montana; Dunn and Parker 1923, 2775.
   L. sp.; Arizona, Colorado, Idaho; Baker 1904, 439.
   Sciurus hudsonicus richardsoni; Montana; Ibid.
   S. floridanus alacer; Oklahoma; Ward 1934, 83.
   S. nuttalli n.; Montana; Dunn and Parker 1923, 2775.
C. i. interrupta; Jordan 1925
   Sylvilagus bachmani b.; California; Jordan 1925, 103.

Cediopsylla simplex (Baker 1895)

    Lepus sp.; North Carolina ; Shaftesbury 1934, 253.

    Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 83.

    S. f. floridanus; Eastern United States ; Jordan 1925, 103.

    S. f. mallurus; North Carolina ; Shaftesbury 1934, 253.

Ceratophyllus adustus Jordan 1932

    Erethizon epixanthum c.; Canada ; Jordan 1932, 255.

C. apachensis Fox 1914

    Cynomys ludovicianus arizonensis; New Mexico ; Fox 1914, 15.

C. divisus (Baker 1898)

    Sciurus fremonti f.; Colorado ; Baker 1904, 441.

    S. hudsonicus richardsoni; Montana ; Dunn and Parker 1923, 2775.

C. multidentatus Fox 1909

    Microtus californicus c.; California ; Fox 1909, 107.

C. niger inflexus Jordan 1929

    Eutamias sp.; Colorado ; Jordan 1929, 37.

C. n. niger Fox 1908

    Rattus norvegicus; California ; Fox 1908, 434.

C. stimsoni Fox 1914

    Thomomys sp.; California ; Fox 1914, 14.

C. terinus Baker

    Citellus columbianus c.; United States ; Baker 1905.

Conorhinopsylla stanfordi Stewart 1930

    Sciurus hudsonicus h.; New York ; Stewart 1930, 179.

Ctenocephalides canis (Bouche 1835)

    Lepus sp.; North Carolina ; Ibid.

    Mus musculus; California ; Fox 1908, 1371.

    Oryctolagus cuniculus domesticus; North Carolina ; Shaftesbury 1934, 252.

    Rattus norvegicus; Fox 1908, 1371.

    R. rattus rattus; Ibid.

Ctenocephalides felis (Bouche 1835)

    Glaucomys volans v.; North Carolina ; Shaftesbury 1934, 252.

    Lepus californicus c.; Arizona ; Vorhies and Taylor 1933, 550.

    Oryctolagus cuniculus domesticus; United States ; Schwartz and Shook 1933, 10.

    Rattus norvegicus; California ; Fox 1909, 1371.

    Sylvilagus floridanus alacer; Oklahoma ; Ward 1934, 83.

    S. f. mallurus; North Carolina ; Shaftesbury 1934, 252.

Ctenocephalus gigas (Kirby)

    Lepus sp.; Michigan ; Baker 1904, 421.

Ctenophthalmus genalis Baker 1904

    Geomys bursarius; Michigan ; Baker 1904, 424.

C. pseudagyrtes Baker 1904

    Evotomys gapperi g.; Pennsylvania; Jordan 1928, 186.

    Geomys bursarius; Michigan; Baker 1904, 421.

    Microtus drummondi; Canada; Baker 1905, 154.

    M. pennsylvanicus p.; New York; Jordan 1928, 186.

    M. sp.; North Carolina; Shaftesbury 1934, 254.

    Mus musculus m.; Pennsylvania; Jordan 1928, 186.

    Neotoma pennsylvanica; Pennsylvania; Ibid.

    Pitymys pinetorum p.; Plimmers Island; Ibid.

    Peromyscus leucopus l.; Ibid.

Ctenopsyllus alpinus (Baker 1895)

    Neotoma sp.; Colorado; Baker 1904, 452.

C. catatina Jordan 1928

    Microtus pennsylvanicus p.; Jordan 1929a, 174.

C. mexicanus (Baker 1896)

    Rattus rattus r.; Mexico; Baker 1904, 452.

C. ravalliensis Dunn and Parker 1923

    Neotoma cinerea c.; Montana; Dunn and Parker 1923, 2775.

C. segnis (Schonherr 1816)

    Mus musculus m.; United States; Fox 1908c, 1371.

    Rattus norvegicus; Ibid.

    Rattus rattus rattus; Ibid.

    Sigmodon hispidus h.; North Carolina; Shaftesbury 1934, 256.

C. selensis (Rothschild 1908)

    Evotomys gapperi g.; Canada; Rothschild 1906, 324.

    Microtus drummondi; Canada; Ibid.

    Peromyscus maniculatus m.; Tennessee; Shaftesbury 1934, 257.

Dactylopsylla comis Jordan 1929

    Thomomys fuscus f.; Canada; Jordan 1929, 38.

Diamanus montanus (Baker 1895)

    Citellus sp.; Baker 1906, 162.

    Otospermophilus grammarus beecheyi; California; Fox 1908, 1565.

    Rattus norvegicus; California; Fox 1908, 1565.

    Sciurus aberti a.; Colorado; Baker 1904, 445.

    S. sp.; Jordan and Rothschild 1914, 259.

Dolichopsylla stylosus (Baker 1903)

    Aplodontia rufa r.; Oregon, Baker 1904, 447.

Doratopsylla blarinae Fox 1914

    Mus musculus m.; Pennsylvania; Jordan 1928, 186.

    Peromyscus leucopus l.; Ibid.

Echidnophaga gallinacea (Westwood 1875)

    Mus musculus m.; California; Fox 1909, 1371.

Rattus norvegicus; North Carolina ; Shaftesbury 1934, 248.

R. rattus rattus; California ; Fox 1909, 1371.

Foxella ignotus apachensis (Baker 1895)

   Thomomys talpoides agrestis; Colorado ; 1915, 56.

F. ignotus ignotus (Baker 1895)

   Geomys bursarius; Iowa ; Jordan 1929, 33.

   Thomomys talpoides t.; Ibid.

F. ignotus fransciscanus (Roths 1910)

   Otospermophilus grammurus beecheyi; California ; Jordan and Rothschild 1915, 45-60.

   Thomomys bottae b.; California ; Jordan and Rothschild 1915, 45-60.

F. ignotus recula (Baker 1895)

   Thomomys talpoides t.; Canada ; Jordan and Rothschild 1913, 56.

Hoplopsyllus affinis Baker 1905.

   Lepus alleni a.; Arizona ; Vorhies and Taylor, 550.

   L. bairdii b.; Montana ; Dunn and Parker 1923, 2775.

   L. californicus melanotis; Colorado ; MacCampbell 1926, 12.

   L. sp. ; Baker 1904, 32.

   Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.

H. anomalus Baker 1903

   Lepus californicus californicus; Oklahoma ; Ward 1934, 83.

   Oryctolagus cuniculus domesticus; United States ; Schwartz and Shook 1933, 12.

   Otospermophilus grammurus beecheyi; United States ; Brumpt 1922, 828.

   Rattus norvegicus; California ; Fox 1908, 1565.

   Sylvilagus aquaticus; Oklahoma ; Ward 1934, 83.

H. foxi Ewing 1924

   Sylvilagus bachmani; California ; Ewing 1924, 350.

H. glacialis (Tasch 1880)

   Lepus arcticus a.; Greenland ; Jordan 1932, 117.

H. glacialis lynx (Baker 1904)

   Lepus americanus macfarlani; Canada ; Jordan 1932, 253.

Hystrichophylla americana Baker 1899

   Evotomys gapperi g.; Maine ; 1904, 454.

   E. sp.; Maine ; Baker 1904, 432, 454.

H. sp.

   Microtus californicus c.; California ; Fox 1909, 11.

H. dippiei Rothschild

   Eutamias luteiventris; Montana ; Dunn and Parker 1923, 2775.

   Peromyscus maniculatus austerus; Ibid.

   Sciurus hudsonicus richardsoni; Montana ; Ibid.

H. gigas (Baker 1904)

   Sylvilagus floridanus f.; Canada, Michigan ; Baker 1904, 450.

H. gigas tahuvuana Jordan 1929
> *Microtus pennsylvanicus p.;* Jordan 1929, 174.
> *Peromyscus leucopus noveboracensis;* New York; Jordan 1933, 65.

H. mammoth Chapin 1921
> *Aplodontia rufa californica;* California; Chapin 1921, 26.

Leptopsylla adelpha Rothschild 1915
> *Mus sp.;* Arizona; Rothschild 1915, 305.

L. hesperomys (Baker 1904)
> *Peromyscus leucopus l.;* Pennsylvania; Jordan 1928, 186.
> *P. leucopus noveboracensis;* New York; Jordan 1933a, 65.
> *P. sp.;* New Hampshire; Baker 1904, 452.

Malareus bitterrootensis (Dunn and Parker 1923)
> *Mus sp.;* Canada; Jordan 1925, 110.
> *Neotoma cinerea cinerea;* Montana; Dunn and Parker 1923, 2775.

M. eremicus (Baker 1904)
> *Peromyscus eremicus e.;* Arizona; Jordan 1933, 442.

M. penicilliger (Grube 1852)
> *Peromyscus maniculatus borealis;* Jordan 1932, 253.

M. sinomus (Jordan 1925)
> *Mus. sp.;* Arizona; Jordan 1925, 180.

M. telchinum (Rothschild 1905)
> *Evotomys gapperi g.;* Baker 1906, 161.
> *Microtus californicus c.;* California; Fox 1909, 10.
> *M. mordax m.;* Dunn and Parker 1923, 2775.
> *Peromyscus maniculatus artemisiae;* Montana; Dunn and Parker 1923, 2775.
> *Sylvilagus nuttalli n.;* Montana; Dunn and Parker 1923, 2775.

Megabothris abantis (Rothschild 1905)
> *Microtus drummondi;* Canada; Baker 1905, 146.

M. asio (Baker 1904)
> *Microtus pennsylvanicus p.;* New York; Jordan 1933a, 62.

M. groenlandicus (Wahlgren 1903)
> *Dicrostonyx groenlandicus;* Greenland; Jordan 1932, 118.

M. lucifer (Rothschild 1905)
> *Microtus drummondi;* Canada; Baker 1905, 149.

M. megacolpus (Jordan 1925)
> *Microtus drummondi;* Canada; Jordan 1929, 33.

> *M. quirini* (Rothschild 1905)
> *Evotomys gapperi g.;* Canada; Baker 1905, 15.
> *E. g. saturatus;* Canada; Baker 1905, 15.
> *Microtus drummondi,* Jordan 1932, 253.
> *Napaeozapus insignis i.;* Jordan 1932, 253.

Megarthroglossus bisetis Jordan and Rothschild 1915
> *Neotoma sp.;* New Mexico; Jordan and Rothschild 1915, 54.

M. longispinosus Jordan and Rothschild 1915.
> *Mus sp.;* Canada; Jordan and Rothschild 1915, 54.
> *Sciurus hudsonicus baileyi;* Canada; Jordan and Rothschild 1915, 52.

Micropsylla peromyscus Dunn and Parker 1923
> *Peromyscus maniculatus artemisiae;* Montana; Dunn and Parker 1923, 2775.

Monopsyllus anisus (Rothschild 1907)
> *Rattus norvegicus;* California; Rothschild 1910a, 94.

M. ciliatus (Baker 1904)
> *Eutamias luteiventris;* Montana; Dunn and Parker 1923, 2775.
> *E. sp.;* California; Baker 1904, 441.
> *Sciurus hudsonicus richardsoni;* Dunn and Parker 1923, 2775.

M. ciliatus protinus (Jordan 1929)
> *Eutamias townsendii t.;* Canada; Jordan 1929, 34.
> *Sciurus hudsonicus h.;* Canada; Jordan 1929, 34.

M. eumolpi eumolpi (Rothschild 1905)
> *Citellus columbiana;* Montana; Dunn and Parker 1923, 2775.
> *Eutamias affinis;* Baker 1906, 162.
> *E. luteiventris l.;* Montana; Dunn and Parker, 2775.
> *Sciurus hudsonicus richardsoni;* Montana; Dunn and Parker 1923, 2775.
> *Microtus drummondi;* California; Jordan 1932, 253.

M. vison (Baker 1904)
> *Citellus columbianus c.;* Montana; Dunn and Parker 1923, 2775.
> *Sciurus hudsonicus h.;* Maine; Baker 1904, 408.
> *S. h. richardsoni;* Montana; Dunn and Parker 1923, 2775.

M. wagneri (Baker 1904)
> *Lepus bairdii b.;* Montana; Dunn and Parker 1923, 2775.
> *Mus musculus;* Idaho; Baker 1904, 405.
> *Peromyscus leucopus l.;* Idaho; Baker 1904, 448.
> *P. maniculatus artemisiae;* Montana; Dunn and Parker 1923, 2775.
> *Sciurus hudsonicus richardsoni;* Montana; Dunn and Parker 1923, 2775.
> *Sylvilagus nuttalli n.;* Montana; Dunn and Parker 1923, 2775.

M. w. systaltus (Jordan 1929)
> *Peromyscus maniculatus arcticus;* Canada; Jordan 1929, 35.

Neopsylla faceta Rothschild 1915
> *Sciurus hudsonicus h.;* Massachusetts; Rothschild 1915, 34.

N. hamiltoni Dunn and Parker 1923
> *Neotoma cinerea c.;* Montana; Dunn and Parker 1923, 2775.

N. inopina Rothschild 1915
> *Citellus columbianus c.;* Montana; Dunn and Parker 1923, 2775.

Evotomys gapperi saturatus; Canada; Rothschild 1915, 32, 44.
Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.
Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.
N. similis
    Peromyscus maniculatus rufinus; New Mexico; Chapin 1919, 59.
N. texanus Stewart 1930
    Rattus norvegicus; Texas; Stewart 1930, 180.
N. wenmanni (Rothschild 1904)
    Neotoma cinerea c.; Canada; Baker 1905, 154.
    Peromyscus leucopus; Massachusetts; Jordan 1928, 186.
    P. leucopus l.; Tennessee; Shaftesbury 1934, 257.
    P. l. noveboracensis; New York; Jordan 1933, 65.
    Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.
Nosopsyllus fasciatus (Bosc 1801)
    Mus musculus; California; Fox 1909, 1371.
    Microtus californicus c.; California; Baker 1904, 440.
    Neotoma pennsylvanica p.; Jordan 1928, 183.
    Peromyscus leucopus l.; Boston; Jordan 1928, 183.
    Rattus norvegicus; North Carolina; Shaftesbury 1934, 255. California;
    Fox 1908, 1371.
    Rattus rattus alexandrinus; Cosmopolitan; Banks 1910, 75.
    R. rattus rattus; Ibid.
    Thomomys bottae b.; Fox 1909, 10.
Nosopsyllus londiniensis (Rothschild 1903)
    Rattus norvegicus; California; Baker 1906, 161.
    R. rattus rattus; California; Banks 1910, 75.
Odontopsyllus charlottensis (Baker 1898)
    Evotomys gapperi saturatus; Canada; Baker 1905, 145.
    Microtus californicus c.; California; Fox 1909, 11.
    Neotoma cinerea c.; Canada; Baker 1905, 162.
    Lepus bairdii b.; Arizona; Dunn and Parker 1925, 2775.
    Peromyscus maniculatus arcticus; Canada; Baker 1905, 162.
    P. leucopus l.; Canada; Ibid.
O. multispinosus (Baker 1898)
    Lepus californicus c.; Oklahoma; Ward 1934, 32.
    Sylvilagus floridanus mallurus; North Carolina; Shaftesbury 1934, 254.
O. spenceri; Dunn and Parker 1923
    Lepus bairdii; Montana; Dunn and Parker 1923, 2775.
    Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.
O. telegoni; Rothschild
    Evotomys gapperi g.; Baker 1905, 146.
    Microtus drummondi; Canada; Tiraboschi 1907, 617.

O. wynuani Fox 1909

    Microtus californicus c.; California; Fox 1909, 241.

Opisocrostis bruneri (Baker 1895)

    Citellus columbianus c.; Colorado, Idaho, Nebraska; Baker 1904, 440.

    C. franklini; Idaho; Nebraska; MacLeod 1933, 112.

    C. richardsoni; Canada; MacLeod 1933, 112.

    C. tridecimlineatus t.; Canada; MacLeod 1933, 112.

    Citellus sp.; Montana; MacLeod 1933, 112.

O. hirsutus (Baker 1895)

    Cynomys ludovicianus l.; Colorado; Baker 1904, 443.

O. saundersi Jordan 1933

    Citellus richardsonii; Canada; Whitehead 1933, 751.

O. tuberculatus (Baker 1904)

    Citellus columbianus c.; Idaho; Baker 1904, 393; Montana; Dunn and Parker 1923, 2775.

    Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.

    Sciurus hudsonicus richardsonii; Montana; Ibid.

Opisodasys keeni (Baker 1896)

    Peromyscus maniculatus keeni; Queen Charlotte Islands; Baker 1904, 444.

O. pseudarctomys (Baker 1904)

    Glaucomys sabrinus alpinus; Montana; Dunn and Parker 1923, 2775.

    Marmota monax m.; New York; Baker 1904, 446.

O. pseudarctomys acasti (Baker 1905)

    Glaucomys sabrinus s.; Canada; Baer 1905, 150.

O. robustus (Jordan 1925)

    Sciurus aberti a.; Jordan 1925, 105.

O. vesperalis (Jordan 1929)

    Glaucomys sabrinus alpinus; Canada; Jordan 1929, 26.

Orchopeas caedens durus (Jordan 1925)

    Sciurus hudsonicus h.; Canada; Jordan 1929, 29.

    S. h. richardsoni; Canada; Jordan 1929, 29.

O. leucopus (Baker 1904)

    Peromyscus leucopus l.; New York; Baker 1904, 445.

    P. l. noveboracensis; Jordan 1933, 62.

O. sexdentatus agilis (Roths 1905)

    Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.

    Neotoma cinerea c.; Canada; Jordan 1929, 30.

    Ochotona princeps; Montana; Dunn and Parker, 1923, 2775.

    Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.

    S. h. baileyi; Canada; Baker 1906, 162.

    Sylvilagus nuttalli n.; Dunn and Parker 1923, 2775.

O. s. pennsylvanicus (Jordan 1928)

    Neotoma pennsylvanica p.; Pennsylvania, Maryland, Virginia; Jordan 1928, 184.

O. s. schisentus (Jordan 1929)

    Neotoma sp.; Arizona; Jordan 1929, 31.

O. wickhami (Baker 1895)

    Erethizon epixanthum e.; Minnesota; Jellison 1933, 43.

    Eutamias luteiventris; Montana; Dunn and Parker 1923, 2775.

    Evotomys gapperi saturatus; Baker 1905, 150.

    Glaucomys volans v.; North Carolina; Shaftesbury 1934, 252.

    Marmota monax m.; Pennsylvania; Jordan 1928, 183.

    Sciurus carolinensis c.; Arizona, Georgia, Iowa, Nebraska, Michigan, New York; Baker 1904, 448.

    S. fremonti f.; Baker 1904, 448.

    S. hudsonicus h.; United States; Baker 1904, 448.

    Sciurus h. richardsoni; Montana; Dunn and Parker, 2775.

    Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 83.

    Peromyscus maniculatus arcticus; Baker 1906, 162.

Oropsylla alaskensis (Baker 1904)

    Citellus parryii kennicotti; Alaska; Baker 1904, 394, 440.

O. arctomys (Baker 1904)

    Marmota monax; New York; Baker 1904, 440.

    M. m. rufescens; New York; Jordan 1933a, 62.

O. idahoensis (Baker 1904)

    Callospermophilus lateralis cinerascens; Montana; Dunn and Parker 1923, 2775.

    Citellus columbianus c.; Idaho; Baker 1904, 413.

    C. nebulicola; Alaska; Fox 1927, 212.

    Lepus bairdii b.; Montana; Dunn and Parker 1923, 2775.

    Marmota flaviventris; Montana; Dunn and Parker 1923, 2775.

    Neotoma cinerea c.; Montana; Dunn and Parker 1923, 2775.

    Sciurus aberti a.; Arizona, Alberta; Baker 1905, 150.

    Sciurus hudsonicus richardsoni; Montana; Dunn and Parker 1923, 2775.

    Sylvilagus nuttalli n.; Montana; Dunn and Parker 1923, 2775.

O. rupestris (Jordan 1929)

    Citellus richardsoni; Canada; Jordan 1929, 32.

    Thomomys sp.; Canada; Jordan 1929, 32.

Phalacropsylla arachis Jordan 1929

    Dipodomys merriami m.; Arizona; Jordan 1929, 38.

P. paradisea; Jordan and Rothschild 1915

    Mus sp.; Rothschild 1916, 33.

    Rattus sp.; Arizona; Fox 1925, 217.

P. shannoni Jordan 1929

    Perognathus sp.; Washington; Jordan 1929, 39.

Pulex sp.

    Lepus californicus melanotis; Colorado; MacCampbell 1926, 12.

P. dugesii Baker 1899

    Lepus californicus c.; Oklahoma; Ward 1934, 83.

    Sylvilagus floridanus alacer; Oklahoma; Ward 1934, 32.

P. irritans Linnaeus 1758

    Lepus sp.; North Carolina; Shaftesbury 1934, 250.

    Oryctolagus cuniculus domesticus; Ibid.

    Rattus norvegicus; California; Fox 1908, 1371.

    R. rattus r.; California; Fox 1908, 1371.

    Sciurus carolinensis c.; North Carolina; Shaftesbury 1934, 350.

    Sylvilagus floridanus mallurus; North Carolina; Shaftesbury 1934, 250.

Rhadinopsylla sectilis Jordan and Rothschild 1923

    Mus sp.; Canada; Jordan and Rothschild 1923, 315.

Rhopalopsyllus dunni Jordan and Rothschild 1922.

    Sigmodon hispidus chiriquensis; Panama; Jordan and Rothschild 1923a, 337.

R. qwyni Fox 1914

    Rattus norvegicus; Georgia; Fox 1914, 11.

R. sigmodoni Stewart 1930

    Rattus norvegicus; Texas; Stewart 1930, 177.

    Sigmodon hispidus h.; Texas; Stewart 1930, 177..

Stenoponia wetmorei Chapin 1922

    Peromyscus leucopus l.; Virginia; Shaftesbury 1934, 248.

    P. l. noveboracensis; Canada; Chapin 1922, 54.

Tarsopsylla coloradensis (Baker 1895)

    Sciurus fremonti f.; Colorado; Baker 1904, 441.

Thrassis acamantis (Rothschild 1905)

    Marmota flaviventris f.; Montana; Dunn and Parker 1923, 2775.

    Marmota f. avara; Montana; Dunn and Parker 1923, 2775.

T. arizonensis (Baker 1898)

    Neotoma albigula a.; Arizona; Baker 1904, 440.

    Citellus sp.; Arizona; Baker 1904, 412, 446.

T. arizonensis littoris (Jordan 1929)

    Citellus tridecimlineatus t.; California; Jordan 1929, 31.

T. bacchi (Rothschild 1905)

    Citellus tridecimlineatus texianus; Baker 1906, 162.

T. fotus (Jordan 1925)

    Citellus tridecimlineatus t.; Colorado; Stewart 1930, 152.

T. francisi (Fox 1924)

    Citellus mollis mollis; Utah; Fox 1927, 211.

T. gladiolis (Jordan 1925)

    Ammospermophilus leucurus cinnamoneus; Utah; Jordan 1930, 269.

    Citellus tridecimlineatus t.; California; Jordan 1925, 108.

    Perognathus sp.; California; Jordan 1925, 108.

T. gladiolis caducus (Jordan 1930)

    Ammospermophilus leucurus cinnamoneus; Utah; Jordan 1930, 269.

T. howelli

    Marmota flaviventris sierrae.

T. pansus (Jordan 1925)

    Citellus sp.; Arizona; Jordan 1925, 109.

Xenopsylla cheopis (Rothschild 1903)

    Mus musculus m.; North Carolina; Shaftesbury 1934, 250.

    Rattus norvegicus; Cosmopolitan; Shaftesbury 1934, 250.

    Rattus rattus; Cosmopolitan; Fox 1908, 1371.

    Sigmodon hispidus h.; North Carolina; Shaftesbury 1934, 249.

HEMIPTERA

Triatoma protracta (Uhler 1894)

    Neotoma fuscipes streatori; Utah; Brumpt 1922, 811.

HYMENOPTERA

Brachymeria fonscolombei (Dufour)

    Lepus californicus texianus; Texas; Roberts 1933, 158.

DIPTERA LARVAE

Bogeria buccata

    Mus musculus; Ohio; Miller 1928, 13.

B. ruficus Austen 1933

    Lepus sp.; Arizona, Colorado, New Mexico, Oregon; Austen 1933, **713**.

Cochliomyia macellaria Fab.

    Lepus californicus texianus; Texas; Roberts 1933, 157.

Cuterebra aldrichi Austen 1933

    Neotoma fuscipes f.; California; Austen 1933, 705.

C. americana Townsend

    Lepus alleni a.; Arizona; Vorhies and Taylor 1933, 550.

    L. californicus c.; Arizona; Ibid.

C. cuniculi Townsend

    Oryctolagus cuniculus domesticus; United States; Schwartz and Shook 1933.

C. emasculator Fitsch 1859

    Sciurus hudsonicus petulans; Seguy 1924, 365.

    S. h. hudsonius; Bau 1906, 25.

    S. carolinensis leucotis; Seguy 1924, 355.

    Tamias striatus lysteri; Canada; Cameron 1926, 430.

C. fontinella Clark

    Peromysous leucopus l.; North Carolina ; Harkema, this paper.

    P. l. noveboracensis; Boston ; Johnson 1930, 283.

    Sylvilagus floridanus mallurus; Smith 1908, 270.

    S. nuttalli n.; New Mexico ; Seguy 1924, 366.

C. grisea Coquilliet

    Mus musculus; Canada ; Cameron 1926, 431.

C. lepusculi Townsend 1897

    Sylvilagus nuttalli n.; New Mexico ; Seguy 1924, 366.

C. princeps

    Lepus alleni a.; Arizona ; Vorhies and Taylor 1933, 550.

    L. californicus c.; Arizona ; Ibid.

    L. callotis; Bau 1906, 27.

C. scudderi Townsend

    Lepus californicus texianus; Texas ; Roberts 1933, 157.

C. tenebrosa Coquilliet

    Cynomys ludovicianus l.; Montana ; Parker and Wells 1919, 101.

    Neotoma cinerea c.; Montana ; Parker and Wells 1919, 100.

    Onychomys leucogaster arcticeps; Montana ; Ibid.

C. sp.

    Lepus artemisia; New Mexico ; Townsend 1892, 299.

    Neotoma fuscipes macrotis; California ; Gander 1929, 57.

    Oryctolagus cuniculus domesticus; United States ; Schwartz and Shook 1933.

    Rattus norvegicus; Canada ; Cameron 1926, 432.

    Sylvilagus floridanus alacer; Oklahoma ; Leonard 1933, 270.

    S. nuttalli n.; New Mexico ; Townsend 1892, 299.

    S. palustris p.; Brauer 1803, 224-228.

Dermatobia sp.

    Lepus callotis; New Mexico ; Townsend 1892, 299.

D. cyaniventris Macquart 1849

    Lepus callotis; Seguy 1924, 366.

D. hominis (Linnaeus)

    Dasyprocta punctata dariensis; Panama ; Dunn 1934, 225.

    D. p. isthmica; Panama ; Ibid.

Sarcophaga plinthopyga Wied.

    Lepus californicus texianus; Texas ; Roberts 1933, 157.

S. sulcata Aldrich

    Lepus californicus texianus; Texas ; Roberts 1933, 158.

Wohlfahrtia vigil (Walker)

    Sylvilagus floridanus mallurus; Johannsen 1926, 156.

APPENDIX II

DESCRIPTION OF A NEW SPECIES OF NEMATODE FROM THE WHITE-FOOTED MOUSE

A nematode is described in this section. This parasite belongs to the family Oxyuridae Cobbold 1864, subfamily Syphaciinae Railliet 1916, and genus SYPHACIA Seurat 1916. For this species the name *Syphacia peromysci* is proposed. Dr. B. G. Chitwood of the Bureau of Animal Industry, United States Department of Agriculture, kindly examined the specimens and diagnosed them as a new species of SYPHACIA.

Syphacia peromysci nov. sp.

Members of the genus SYPHACIA are slender, milk white forms. The male is much smaller than the female and the tail of both sexes is long and slender. The cuticle is coarsely striated transversely. The mouth is provided with
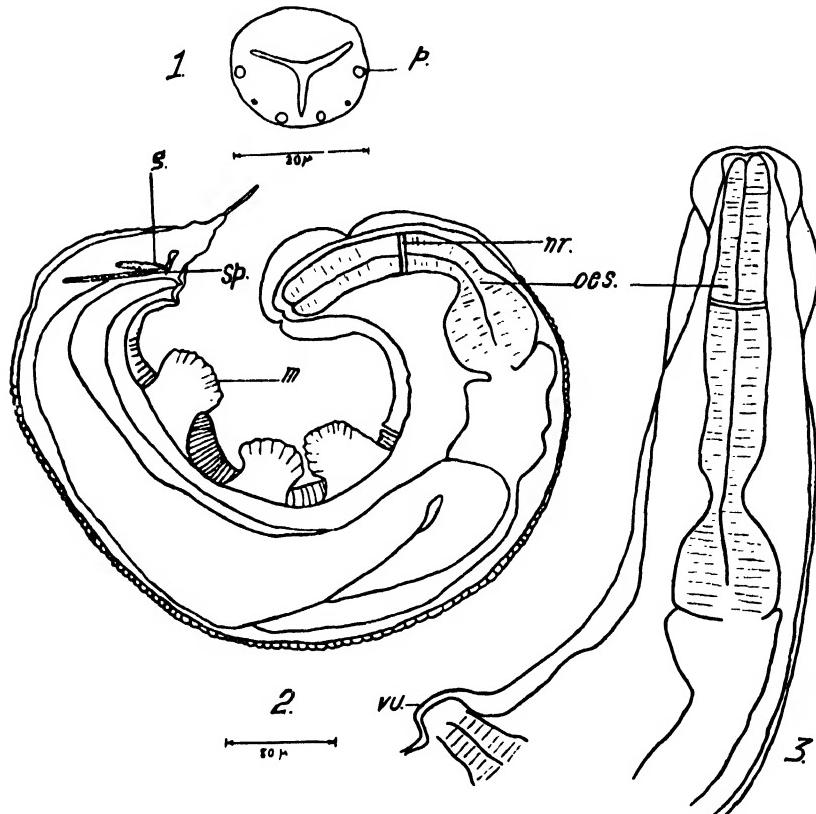
FIG. 5. *Syphacia peromysci* nov. sp.; 1. Head, end face view; 2. Adult male, entire; 3. Adult female, anterior end.

g — gubernaculum	nr — nerve ring	sp — spicule
m — mamelon	oes — oesophagus	vu — vulva
	p — papilla	

three lips of about equal size. The circumoral papillae are situated laterally in two groups consisting of a large papilla situated on each side of a smaller submedian one (Fig. 5, 1).

The male is 913 micra to 1.3 mm. long and 120-124 micra wide. The cuticle of the anterior end is inflated and extends to the cervical papillae. The oesophagus is typically oxyuroid, 140 to 150 micra long by 30 micra wide. The oesophageal bulb is spherical, 66 to 80 micra in diameter and is joined to the oesophagus by a slender constriction. The nerve ring surrounds the oesophagus approximately 90 micra from the anterior end of the oesophagus. The excretory pore opens ventrally approximately 172 micra from the anterior end of the body. The cervical papillae are situated approximately 60 micra from the head. Lateral alae are present beginning at the cervical papillae. There are two small symmetrical bursal alae and three pairs of caudal papillae. The spicule is simple, 70 micra long and 3 to 4 micra wide. The gubernaculum is 37 micra long by 5 micra wide and the accessory piece is 20 micra long. The ventral surface of the body bears three striated mamelons, which extend approximately 27 micra beyond the cuticle. They are approximately 50 micra long (Fig. 5, 2).

The female is 2 to 2.5 mm. long with a maximum width of 0.172 mm. The oesophagus including the bulb is 353 micra long by 46 micra wide at the widest point. The oesophageal bulb is 80 micra in diameter. The nerve ring is 97 micra from the anterior end of the oesophagus. The anus is situated 525 to 700 micra from the tip of the tail. The vulva is situated on a cuticular prominence 507 to 534 micra from the anterior end (Fig. 5, 3). The eggs are oval 80 to 81 micra long by 24 micra wide.

Host: *Peromyscus leucopus leucopus.*

Location: Caecum.

Locality: Duke Forest, Durham, North Carolina.

Syphacia peromysci resembles *Syphacia obvelata* (Rudolphi 1802), the type species of the genus, in body form and the number of mamelons in the male. It differs in that the former species is smaller than the latter in many respects. The mamelons extend beyond the cuticle to a greater distance than do those of *S. obvelata*. The eggs are much larger in the type species being 100 to 142 micra long by 30 to 40 micra wide. *Syphacia peromysci* can be separated from *S. thompsoni* Price 1928 by its smaller size. The species is readily distinguished from *S. pallargi* (Seurat 1915) and *S. pearsei* Baylis 1928 by the number of ventral mamelons, there being but two in these species.

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THE "BIG WOODS" OF MINNESOTA: ITS STRUCTURE, AND RELATION TO CLIMATE, FIRE, AND SOILS

By

Rexford F. Daubenmire

*University of Minnesota,
Minneapolis, Minn.*

CONTENTS

THE "BIG WOODS" OF MINNESOTA: ITS STRUCTURE, AND RELATION TO CLIMATE, FIRE, AND SOILS

INTRODUCTION

Minnesota includes parts of three of the principal plant formations of North America. The southwestern and westerly portions of the state are overlapped by the grasslands. The northeastern corner belongs phytogeographically to the boreal conifer forest. Separating these two is a belt of deciduous forest, extending diagonally across the state from the southeast to the northwest (Fig. 1). The present study concerns a portion of the deciduous forest.

When the early French explorers came into the central part of Minnesota, they recognized a portion of the deciduous forest, some 3,030 square miles in extent, as being decidedly superior to the adjacent woodlands on all sides. The timber was very dense; the trees were much taller and of species different from those of the surrounding oak forest and oak savanna. In referring to this rather definite area they used the names 'Bois Grand' or 'Bois Fort' which shortly thereafter were translated as 'Big Woods' (Fig. 1).

The Big Woods is a forest community dominated by sugar maple (*Acer saccharum* Marsh.)[1] and basswood (*Tilia americana* L.). Although it was not the only stand of sugar maple-basswood forest in Minnesota, the Big Woods was the largest continuous area of such timber in the state. Numerous other tracts occur in the remainder of the deciduous forest, some in contiguous portions of the boreal conifer forest, and some about lakes and large rivers in the adjacent prairie.

Since the term "Big Woods" was apparently applied by the French to a timbered area dominated by sugar maple and basswood, it has often been applied since then to all tracts of this type of forest regardless of their location in Minnesota. The more restricted meaning is used by the writer because it defines the portion of the sugar maple-basswood community which was studied.

With the rapid settling of Minnesota in the last century, the forests have been cleared to such an extent that now the Big Woods is represented only by scattered woodlots, most of which are heavily pastured, and a very few near-virgin stands. The present study is an attempt to analyse from the phytosociological viewpoint the best remnants of the primeval forest which still exist, to reconstruct the original boundaries of the Big Woods, and to solve the distributional problems involved.

[1] The nomenclature for woody plants follows Rosendahl and Butters (1928), and for herbaceous plants, Robinson and Fernald (1908).
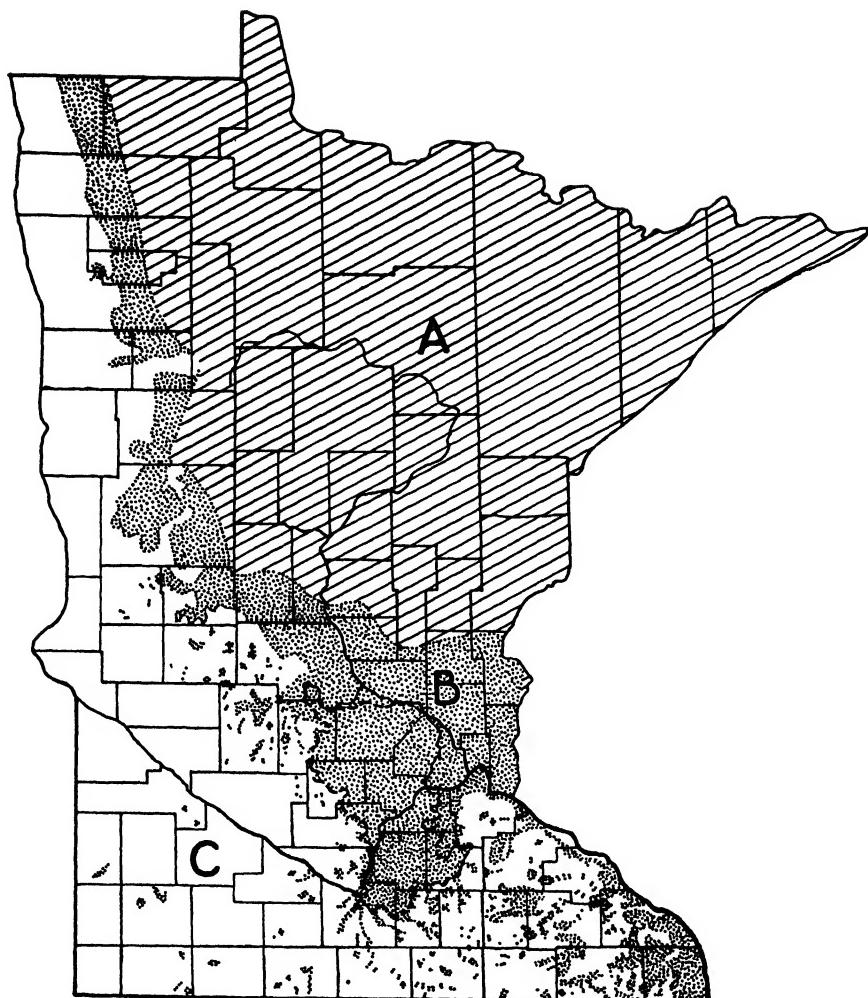
FIG. 1. Principal plant formations of Minnesota, after Upham (1884). The Big
Woods is indicated by the broken line. A. Region characterized by pine subclimax
communities. Climax types are sugar maple-basswood in the south and western parts,
spruce-fir-birch (boreal conifer forest) in the extreme northeastern portion, and fir-
basswood in the intermediate region. B. Region characterized by pure deciduous for-
est, with subclimax communities of oak and aspen, and sugar maple-basswood as
climax. C. Region of tall-grass prairie.

SOCIOLOGY OF THE COMMUNITY

The scarcity of surviving virgin tracts of the Big Woods quite justifies a
study of the original structure of the community based on these remnants
before they too are destroyed.   It has been possible to find and study two
areas of near-virgin stands; one of these, to which I shall refer as the "Minne-
tonka Woods," has suffered a slight period of grazing a number of years ago,

the other, the "Northfield Woods," has been but slightly disturbed by the removal of a few trees.

QUANTITATIVE STUDIES

MINNETONKA WOODS

Two excellent remnants of the Big Woods occur on private estates located near Sunrise Point on the east side of Lake Minnetonka in Hennepin County. The home of the late R. M. Bennett is surrounded by a strip of forest, part of which from all appearances is in perfect state of preservation. Mr. Bennett stated in a letter to the writer, however, that previous to his purchase of the land in April, 1900, this forest was subjected to grazing by sheep and goats for a period which he estimated at four years. Since 1900 the forest has not been disturbed, and in this interval of thirty-five years the community has so completely recovered from the short period of disturbance that there now is no apparent evidence of the pasturing save for the persistence of a few patches of weeds (chiefly Arctium and Acalypha). A similar area of forest occurs about one-eighth mile south of the Bennett woods.

A total of 25 sets of plots was studied in these two pieces of timber at Lake Minnetonka. The locations of all quadrats were predetermined from sketch maps made for the purpose, to eliminate personal judgment in their selection. The distances between the centers of adjacent quadrats varied from 20 to 34 meters. The irregular distribution of the better patches of timber makes impossible an estimate of the total area from which the samples were taken.

Trees 1 inch d.b.h. (diameter breast high, i.e., 4.5 feet above the ground) and over were studied in 25 quadrats, each 10 meters square. In one predetermined corner of each of these larger plots was located a plot 2 x 8 meters. Trees under 1 inch d.b.h and shrubs were studied in these areas. Data concerning the forest floor herbs were derived from 4 plots, 0.25 x 4 meters each, located one in each corner of the 10 x 10 meter plots.

The rectangular or strip plots were used in preference to the usual square on the strength of investigations by Clapham (1932) and Ilvessalo (1922), which seem to indicate that by using the elongate form a smaller area is sufficient to give a true statistical picture of a community than if the square is employed. The elongate form was deemed especially desirable when dealing with the lower life forms, since such species are more frequently grouped into isodiametric 'families' which may coincide with an isodiametric plot or be entirely excluded. Obviously, an elongate plot intercepts more than one of these 'families' more often than would a square plot, and thus gives less erratic results.

Quadrat data concerning the herbs were obtained during the last two weeks of July, 1933. At this time, practically all of the withering elements of the

spring flora could still be counted and identified with ease, and the fall species
were developed sufficiently so that they also could be determined by one ac-
quainted with the flora.

TABLE 1. Density of tree species per 2,500 sq. meters, Minnetonka Woods.

	Individuals less than 1 in. d.b.h.[a]		Individuals 1 in. d.b.h. or over			
	1 ft. tall or less	More than 1 ft. tall	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. or more d.b.h.	Totals
Acer saccharum Marsh.....	12,915	2,453	102	28	25	15,523
Tilia americana L..........	33	17	17	6	16	89
Ulmus fulva Michx........ }	477[a]	55	12	1	4	577
Ulmus americana L........ }		22	1	0	5	
Ostrya virginiana[4] K. Koch.	11	61	21	0	0	93
Quercus borealis maxima Ashe	0	6	1	0	3	10
Celtis occidentalis L.......	50	11	0	0	0	61
Totals	13,486	2,625	154	35	53	16,353

Density. As defined by European plant sociologists, density refers to the
number of individuals of a species which occurs on a given area. Tables 1, 2,
and 3 contains the results of a study of density of the sugar maple-basswood
community at Lake Minnetonka.

On the basis of numbers of mature individuals, this community is quite
properly called a sugar maple-basswood association. Maple reproduces pro-
lifically by seed, and the effects of natural thinning are clearly seen in com-
paring the density figures from left to right. The very low density of bass-
wood in the "seedling" stages appears even more remarkable when it is stated
that even after diligent search the writer did not discover a single basswood
seedling in these woods during the entire growing seasons of 1933 and 1934,
nor any saplings which seemed undoubtedly of direct seedling origin. As a
rule basswood seeds germinate well in this region, but apparently the seedlings
become established only rarely. Once established, however, the individual
seems capable of perpetuating itself indefinitely by basal sprouts. Since the
sprouts of basswood have nearly as great density as the mature trees, it fol-
lows that mortality must be very low. This is a direct consequence of the
manner of reproduction; the young sprouts have a more mature root system
to depend upon for water, and are thus preserved during the dry seasons
which take heavy toll among seedlings. Due to this type of reproduction, all
basal sprouts of Tilia had to be considered as individuals in the plot studies.
The behavior of the two most important trees in this association is thus sharply
contrasted in their methods of reproduction.

The two elms illustrate an example of close ecological similarity between
two species in the same genus.

[a] The figures in this category have been multiplied by the proper figure to compensate for the
smaller sized plot used in obtaining these data.
[a] These species could not always be differentiated at this stage of growth.
[4] A small tree.

The environmental requirements of Celtis seem very close to those of the true climax species, but the conditions maintained in this forest evidently will not permit it to mature. The tree is characteristically a river-terrace species in this region, although I have occasionally seen mature specimens in poorly drained sites of the sugar maple-basswood forest.

TABLE 2. Density of shrub species per 100 square meters (25 plots, 2 x 8 meters each). Minnetonka Woods.

SPECIES	No. of Plants	SPECIES	No. of Plants
Parthenocissus vitacea (Knerr) Greene	147	Zanthoxylum americanum Mill.	16
Celastrus scandens L.	136	Rhus toxicodendron L.	6
Sambucus pubens Michx.	28	Vitis vulpina L.	3
Menispermum canadense L.	28	Rubus occidentalis L.	3
Ribes cynosbati L.	20	Total	387

TABLE 3. Density of herbaceous species per 100 square meters (100 plots, 0.25 x 4 meters each). Minnetonka Woods.

SPECIES	No. of Plants	SPECIES	No. of Plants
Uvularia grandiflora Sm.	812	Arenaria lateriflora L.	17
Osmorhiza claytoni (Mich.) Clarke.	728	Arisaema triphyllum (L.) Schott.	13
Circaea lutetiana L.	377	Botrychium virginianum (L.) Sw.	13
Solidago latifolia L.	215	Actaea rubra (Ait.) Willd.	11
Viola pubescens Ait.	157	Aralia nudicaulis L.	10
Carex pennsylvanica Lam.	148	Desmodium grandiflorum (Walt.) DC.	10
Sanguinaria canadensis L.	141	Sanicula gregaria Bicknell.	9
Amphicarpa pitcheri T. & G.	115	Cryptotaenia canadensis (L.) DC.	7
Maianthemum canadense Desf.	61	Caulophyllum thalictroides (L.) Michx.	5
Smilacina racemosa (L.) Desf.	53	Carex laxiflora latifolia Boott.	4
Thalictrum dioicum L.	46	Smilax herbacea L.	4
Laportea canadensis (L.) Gaud.	45	Ranunculus abortivus L.	3
Phryma leptostachya L.	42	Asplenium filix-femina (L.) Bernh.	2
Hydrophyllum virginianum L.	36	Geranium maculatum L.	1
Galium triflorum Michx.	33		
Polygonatum biflorum (Walt.) Ell.	31		
Alliaria officinalis* Andrz.	27	Total	3,081

Close scrutiny of the quadrat data shows no irregularity which might be taken as evidence of the period of disturbance by grazing which was mentioned previously. Among the several influences which a period of grazing should have had on the forest would be that the seedlings of the trees during these years, together with small trees only a few years old, would have been eaten or trampled, and thus greatly reduced in numbers. Furthermore, as time went on, there would always be one size class represented by a paucity of individuals, and this group would move progressively through the higher classes to the mature size and then be obliterated. A curve based on all indi-

ᵈ This herb is a weed introduced into eastern North America from Europe.

vidual maples in the quadrats, separating the diameter classes into 1-inch intervals, shows a smooth gradual decline with increasing size, which is suggestive of an uninterrupted process of natural thinning. If the grazing had been severe, or of long duration, there should now be an abrupt break in such a curve occurring somewhere about the 5-inch diameter class.

Frequency. In current phytosociological usage, the term frequency is employed to designate the percentage of quadrats, of the total number examined, in which a species occurs. Tables 4, 5, and 6 contain the frequency percentage for all of the vascular plants which occurred in the plots.

TABLE 4. Frequency of the tree species. Minnetonka Woods.

	Individuals less than 1 in. d.b.h.[6]			Individuals 1 in. d.b.h or over[7]	
	1 ft. tall or less	more than 1 ft. tall	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. or more d.b.h.
Acer saccharum	100%	100	80	60	76
Tilia americana	4	4	36	16	48
Ulmus fulva	64[8]	32	24	4	16
Ulmus americana		8	4	0	20
Quercus borealis maxima	0	4	4	0	8
Ostrya virginiana	8	12	28	0	0
Celtis occidentalis	16	8	0	0	0

The predominance of sugar maple is again attested by its high frequency. The sequence of importance among the trees is approximately the same in frequency as in density. The very low frequency of Tilia in the smaller size classes reflects the clustered nature of the basal sprouts.

TABLE 5. Frequency of shrub species (25 plots, 2 x 8 meters each). Minnetonka Woods.

SPECIES	Per Cent	SPECIES	Per Cent
Parthenocissus vitacea	68	Vitis vulpina	12
Sambucus pubens	48	Zanthoxylum americanum	4
Ribes cynosbati	32	Rhus toxicodendron	4
Celastrus scandens	16	Rubus occidentalis	4
Menispermum canadense	12		

Among the shrubs, Celastrus has a very high density, while its frequency rating is relative much lower. This signifies many individuals distributed in groups over the forest. Such a distribution, referred to as "hyperdisperse" by Schustler (see Braun-Blanquet 1932, p. 31), is obvious to anyone who would make even a superficial survey of the forest, yet it is only by the comparison of studies of density and frequency that such a condition can be expressed in tangible form.

Sambucus, by way of contrast, is quite high in frequency and comparatively low in density. Accordingly, the few plants are found well scattered over the forest floor. Schustler refers to this type of distribution as "hypodisperse."

[6] Data derived from 25 plots, 2 x 8 meters each.
[7] Data derived from 25 plots, 10 x 10 meters each.
[8] These species could not always be differentiated at this stage of growth.

TABLE 6. Frequency of herbaceous species (100 plots, 0.25 x 1 meter each).
Minnetonka Woods.

SPECIES	Per Cent	SPECIES	Per Cent
Osmorhiza claytoni	83	Arisaema triphyllum	6
Uvularia grandiflora	64	Laportea canadensis	6
Circaea lutetiana	49	Sanicula gregaria	4
Viola pubescens	45	Caulophyllum thalictroides	4
Sanguinaria canadensis	41	Carex laxiflora latifolia	3
Amphicarpa pitcheri	25	Desmodium grandiflorum	3
Thalictrum dioicum	25	Smilax herbacea	3
Phryma leptostachya	23	Arenaria lateriflora	2
Carex pennsylvanica	19	Alliaria officinalis	2
Smilacina racemosa	16	Cryptotaenia canadensis	2
Maianthemum canadense	13	Ranunculus abortivus	2
Hydrophyllum virginianum	11	Aralia nudicaulis	2
Polygonatum biflorum	11	Actaea rubra	2
Galium triflorum	10	Geranium maculatum	1
Solidago latifolia	10	Asplenium filix-femina	1
Botrychium virginianum	9		

The most important members of the herbaceous flora are not confined to any one seasonal aspect. Uvularia, Viola and Sanguinaria flower in spring, Circaea and Osmorhiza in summer, and Solidago is a characteristic autumnal plant. The last species presents another good example of the hyperdisperse type of distribution, being high in density and low in frequency.

Dominance. Basal area was computed as a measure of relative dominance among the tree species. This analysis is made by converting the diameter breast high into cross-sectional area for each individual 1 inch d.b.h. or over, and then adding up all the individual areas for each species. Table 7 shows the preponderant importance of Acer, with Tilia again second in importance. As in the preceeding studies, the elms are third in importance and the red oak last.

TABLE 7. Basal area of tree species in square feet, per 2,500 square meters, individuals smaller than 1 inch d.b.h. are excluded. Minnetonka Woods.

SPECIES	1-3 inches d.b.h	4-9 inches d.b.h	10 inches or more d.b.h	Total
Acer saccharum	1.5544	5.5143	44.2409	51.3096
Tilia americana	.3710	1.2055	26.8510	28.4275
Ulmus americana	.0055	.0000	9.9797	9.9855
Ulmus fulva	.1582	.2673	6.6649	7.0904
Quercus borealis maxima	.0490	.0000	6.1414	6.1904
Ostrya virginiana	.3353	.0000	.0000	.3353
Total	2.4734	6.9871	93.8779	103.3387

A record of the maximum diameters of the tree species is worthy of inclusion at this point. The following figures represent the d.b.h. of the largest specimens of the species which the writer found on the uplands within the Big Woods region:

	Inches		Inches
Acer saccharum	29	*Ulmus fulva*	20
Tilia americana	30	*Quercus borcalis maxima*	32
Ulmus americana	41	*Ostrya virginiana*	9

The elms in particular attain much larger size with an approach toward poorly drained conditions. In such a habitat I measured one American elm which had a d.b.h of 6 feet 3 inches.

Phytographs have been constructed for the tree species of the Minnetonka Woods. This type of diagram, devised by Lutz (1930), is intended to portray graphically the relative importance of the species.

The larger the area of the trapezium (Fig. 2), the more important the species in the community. The lower radius (No. 3) is very critical as an indicator of the reproductive success of the species. If a species is represented in the plots by all five size classes, the lower angle of the trapezium extends to the edge of the circle. When any one size class is lacking, the trapezium ends four-fifths of the distance to the circle. One serious criticism of this method of showing size classes is that it does not indicate *which* of the classes is absent. An example which illustrates this weakness is as follows: In the Northfield Woods, *Carya cordiformis* K. Koch, reproduces successfully but does not attain a diameter sufficient to give it a place in the largest size class (Table 8), in spite of the fact that it is mature from the reproductive standpoint and is a member of the dominant stratum. A phytograph of this species would show the presence of only four size classes and give the impression that it is not a climax tree. It is important to know whether it is the largest size class, intermediate, or the smallest one which is not represented in the forest.

The first three of the species shown in the phytograph are apparently stable. The same is true of Ostrya; the poor representation in the phytograph reflects the limited size of the mature trees. *Ulmus fulva* and the oak, according to the diagram, do not appear to be reproducing successfully, but such is not the case. For these species, which have low density but also low mortality, the number of plots studied covered an area insufficient to include all size classes.

Floristic list of the Minnetonka Woods. An attempt was made to compile a complete species list of all the trees, shrubs, and herbs which occur in the least-disturbed parts of this forest. Aside from those recorded in the plots, no additional tree species were found, and only one shrub, *Prunus virginiana* L., can be added to the shrub list. Among the herbs, the following list should be added to the group for which density and frequency have been given: *Allium tricoccum* Ait., *Anemone quinquefolia* L., *Aplectrum hyemale* (Muhl.) Torr., *Aquilegia canadensis* L., *Aralia racemosa* L., *Eupatorium urticaefolium* Reichard., *Galium aparine* L., *Hepatica acutiloba* DC., *Panax quinquefolium* L., *Sanicula marilandica* L., *Trillium cernuum* L., *Viola canadensis* L.

Acer saccharum   *Tilia americana*   *Ulmus fulva*

Ulmus americana   *Ostrya virginiana*   *Quercus borealis maxima*
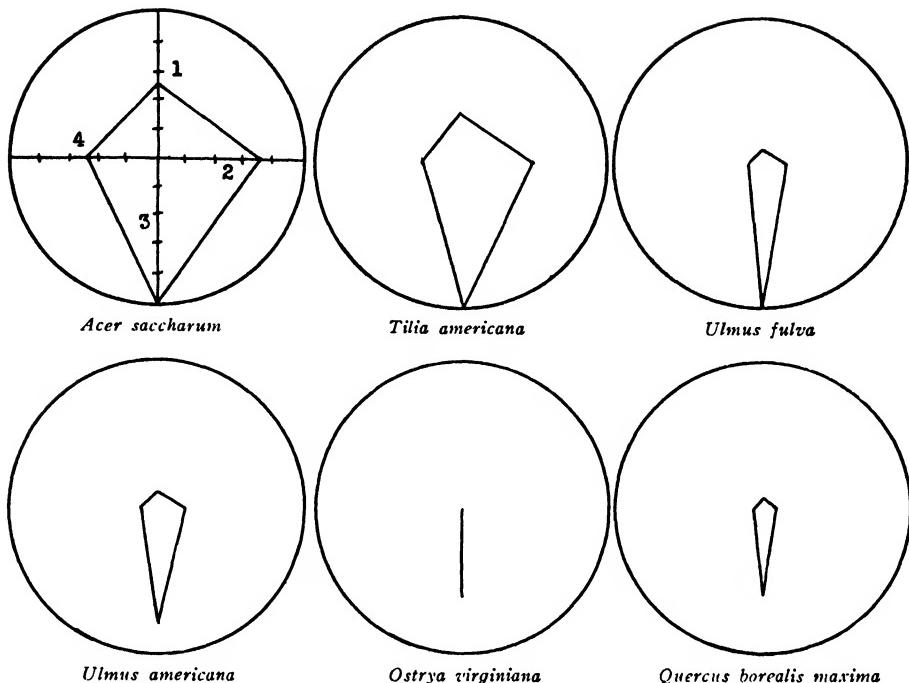
FIG. 2. Phytographs of the tree species in the Minnetonka Woods. The inner end of each radius represents 0 for each of the 4 sociological characteristics:

Radius 1. Density:[9] each species representing a percentage of the total density of stems 10 inches d.b.h. and over.

Radius 2. Frequency: percentage of the 25 quadrats (10 x 10 meters) in which stems 10 inches d.b.h. or over occurred.

Radius 3. Size classes: number of size classes, as separated in Table 1, by which the species is represented.

Radius 4. Dominance (as measured by basal area): each species represented as a percentage of the total basal area of all stems 10 inches d.b.h. and over which occurred in the quadrats.

The figures for which the phytograph for Acer is based, for example, are: density 47 per cent, frequency 76 per cent, size classes 5, basal area 47 per cent.

NORTHFIELD WOODS

In making reconnaissance surveys of many isolated stands of the Big Woods, it became apparent that while quite a number of stands seem to have once been identical in composition with the Minnetonka Woods, others differed in having a wider variety of tree species. The Northfield Woods seemed quite representative of this richer type of community and since it seemed to be the least cut over of the ungrazed remnants, it was chosen for special study. The stand is located in Rice County just opposite the southwest corner of Dakota County, approximately 35 miles south-southeast of the Minnetonka Woods (see location in Fig. 4).

[9] In the original description of the phytograph, Lutz did not differentiate between "density" which is statistically exact, and "abundance" which is an estimate of density. Apparently he used density data and referred to them as "abundance."
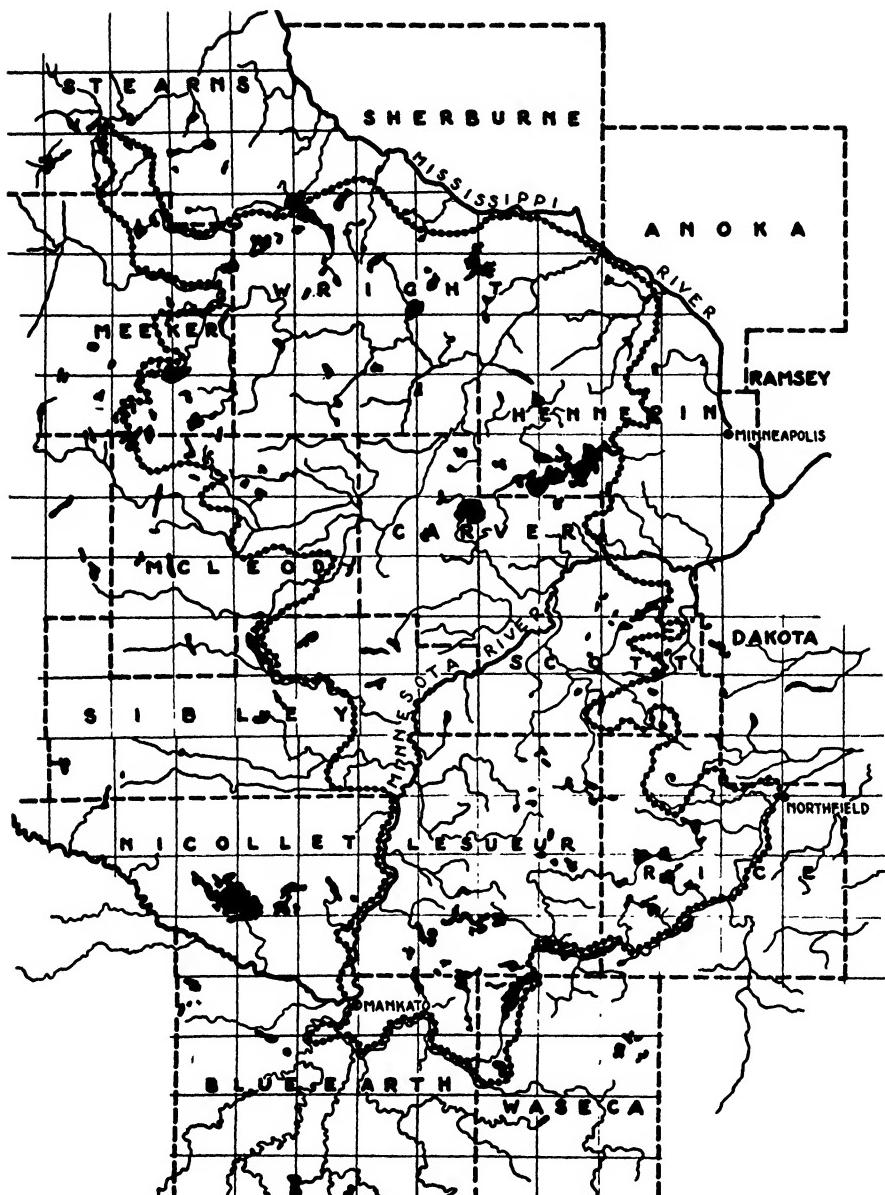
FIG. 3. Detailed map of the Big Woods showing the relation of certain parts of the forest boundaries to lakes and streams.

In the summer of 1934, twenty-five 10 x 10 meter quadrats were studied, together with an equal number of 2 x 8 meter areas. Only the tree species were considered. The data have been analyzed so that tables for density, frequency, and basal area (Tables 8, 9, and 10) are directly comparable to those concerning the Minnetonka Woods.
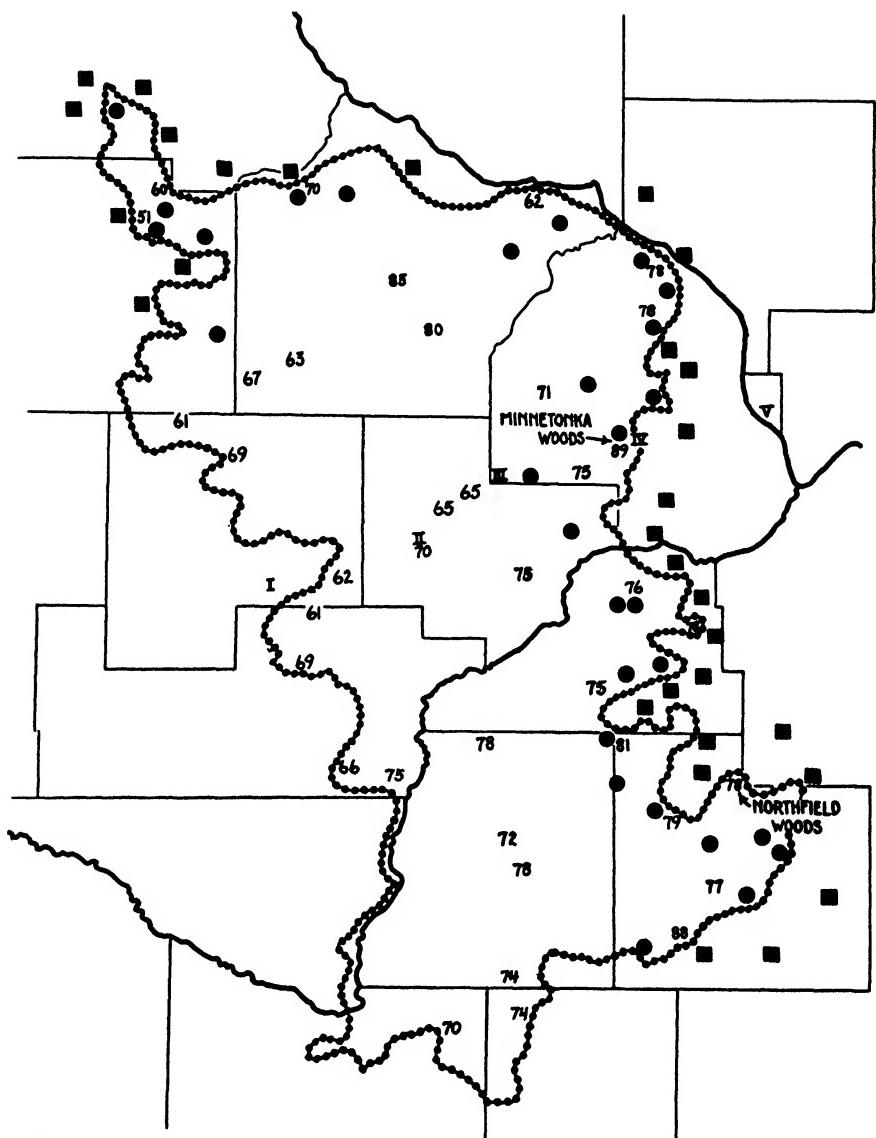
FIG. 4. Outline map of the Big Woods showing location of forest height ·
measurements, the 5 climatological stations (indicated by Roman numerals), the Min-
netonka and Northfield Woods, and the stations where soils were tested in the Mixed
Oak Forest (indicated by squares) and in the Big Woods (indicated by circles).

Several marked differences are apparent when the data for the two forests
are compared. The six tree species which complete the list of the Minnetonka
community are also the principal dominants of the Northfield Woods, but
they are accompanied by *Fraxinus pennsylvanica, F. pennsylvanica lanceolata,
Carya cordiformis,* and *Quercus macrocarpa olivaeformis*. According to the

plot data, *Acer negundo* germinates but does not mature here—a parallel to the behavior of Celtis at Lake Minnetonka. Bur oak, with only one seedling and no intermediate sizes, is definitely not a member of the climax community in the strict sense, but probably owes its existence to local openings in the forest which occasionally permit the species to gain a foothold. Aside from the species recorded in the plots, *Juglans cinerea* L. also occurs here. This piece of timber, then, is dominated by the same species, and in nearly the same proportion, which compose the Minnetonka Woods, but has in addition four other species which seem to be integral parts of the mature community.

TABLE 8. Density of tree species per 2,500 square meters. Northfield Woods.

	Individuals less than 1 in. d.b.h.[10]		1-3 in. d.b.h.	Individuals 1 in. d.b.h. or over		Totals
	1 ft. tall or less	more than 1 ft. tall		4-9 in. d.b.h.	10 in. or more d.b.h.	
Acer saccharum	400	837	58	46	15	1,356
Tilia americana	0	19	1	8	26	54
Quercus borealis maxima	31	0	0	3	12	46
Ulmus americana ....⎱	⎰ 131[11]	6	5	1	6	230
Ulmus fulva ....⎰		75	3	3	0	
Ostrya virginiana	0	0	11	4	0	15
Fraxinus pennsylvanica						
lanceolata Sarg.	31	144	1	1	2	179
Fraxinus pennsylvanica Marsh.	0	12	0	0	1	13
Carya cordiformis	444	31	2	3	0	480
Quercus macrocarpa						
olivaeformis Gray.	6	0	0	0	1	7
Acer negundo L.	6	12	0	0	0	18
Totals	1,049	1,136	81	69	63	2,398

TABLE 9. Frequency of tree species. Northfield Woods.

	Individuals less than 1 in. d.b.h.[12]		1-3 in. d.b.h.	Individuals 1 in. d.b.h. or over[13]	
	1 ft. tall or less	more than 1 ft. tall		4-9 in. d.b.h.	10 in. or more d.b.h
Acer saccharum	56	96	72	72	48
Tilia americana	0	4	4	24	52
Quercus borealis maxima	20	0	0	12	36
Ulmus americana ....⎱	⎰ 32[11]	4	12	4	24
Ulmus fulva ....⎰		20	16	8	0
Ostrya virginiana	0	0	20	8	0
Fraxinus pennsylvanica lanceolata	20	44	4	4	8
Fraxinus pennsylvanica	0	8	0	0	4
Carya cordiformis	68	16	8	8	0
Quercus macrocarpa olivaeformis	4	0	0	0	4

[10] The figures in this category have been multiplied by the proper figure to compensate for the smaller size plot used in obtaining these data.
[11] These species could not always be differentiated at this stage of growth.
[12] Data derived from 25 plots, 2 x 8 meters each.
[13] Data derived from 25 plots, 10 x 10 meters each.
[14] These species could not always be differentiated at this stage of growth.

TABLE 10. Basal area of tree species in square feet per 2,500 square meters. Individuals smaller than 1 inch are excluded. Northfield Woods.

	1-3 in. d.b.h.	4-9 in. d.b.h.	10 in. d.b.h. or over	Totals
Acer saccharum	1.77	9.01	14.41	25.19
Tilia americana	.01	2.10	50.19	52.30
Quercus borealis maxima	.00	.67	19.24	19.91
Ulmus americana	.12	.44	7.48	8.04
Ulmus fulva	.03	.71	.00	.74
Ostrya virginiana	.36	.38	.00	.74
Fraxinus pennsylvanica lanceolata	.02	.09	4.82	4.93
Fraxinus pennsylvanica	.00	.00	1.07	1.07
Quercus macrocarpa olivaeformis	.00	.00	1.77	1.77
Carya cordiformis	.04	.53	.00	.57
Totals	2.35	13.93	98.98	115.26

A second comparison concerns the reversal of the relative importance of Tilia and Acer in certain size classes. In the two larger size classes, Tilia is conspicuously the more important in density, frequency and dominance. However, since the maple predominates in all the other size classes, and since no maples occurred over 18 in. d.b.h (while basswoods were found ranging up to 30 in.) it seems quite probable that the maple has at some time been disturbed either by selective cutting, or possibly injured by use in making maple sugar. There are stumps in the forest, and some of them are quite large, so that selective cutting alone might account for this paucity of large maples.

A third conspicuous feature of this forest is the relative scarcity of very young reproduction. The second size class (over 1 foot tall, yet under 1 inch d.b.h.) is better represented than the seedling stage in the maple, ashes, and box elder. This suggests that some factor may have recently interfered with the germination and establishment of seedlings. Perhaps the unusually severe drought of the latter part of May 1934, was responsible for much of this destruction of seedlings. The atmometric evaporation for this critical period within the Minnetonka Woods was exceedingly high, and must have been fatal to a large percentage of seedlings. Atmometers 1.5 meters above the forest floor lost 891 cc. from May 19 to June 2, whereas the average loss for equal periods during the remainder of the growing season was 296 cc. For this unusual period evaporation was higher within this mesic forest than it usually is on the open prairie immediately west of the Big Woods.

The total basal area of the Northfield Woods is a little greater than that of the Minnetonka Woods in spite of the cutting in the former.

This comparative study of the two samples of the Big Woods shows that even though the composition of the sugar maple-basswood community varies, six species are usually the most important, and bear the same approximate relationships to each other. Extensive but more superficial studies over the entire area further substantiate this conclusion.

FIG. 5. Minnetonka Woods in winter aspect.

FIG. 6. A large bur oak surrounded by young sprout forest composed chiefly of basswood and ironwood. Hennepin County, Minn.

While working in the Northfield Woods, the writer on several occasions noticed a tendency toward layering in both sugar maple and slippery elm (*Ulmus fulva*)—species in which the habit has not, to the writer's knowledge, been previously reported. A specimen of the maple which I preserved may be described as follows: A slender branch, originating from the base of a maple 4 inches d.b.h., about 2 cm. above the ground line, ran horizontally just beneath the litter and duff for 3 dm. and then forked. One division extended 1 dm. and the other 2 dm. further, then both turned erect. In addition, there were two other erect branches arising from the horizontal shoot at a point 1.5 dm. from its base. Roots were produced abundantly from the lower side of the prostrate stem, but only on the longer of the two creeping branches. A similar case was found in the elm, except that here the prostrate branch had arisen from a smaller parent, the aerial portions of which had in the meantime died.

QUALITATIVE ANALYSES (MINNETONKA WOODS)

Periodicity. During the growing season of 1934, the Minnetonka Woods was visited repeatedly at intervals seldom exceeding 2 weeks for the purpose of taking phenological notes.

Leaf buds of the trees were opening on April 29, and at the same time the first herbs (Sanguinaria and Hepatica) were found in bloom. Approximately 3 weeks were required for the completion of the canopy, which remained fully complete for about 15 weeks of the summer. On September 14 the leaves began to drop, and flowering among the herbs likewise ceased at about this time. By October 6 the trees were again bare.

A study of the periodicity among the herbaceous species over the entire year brings out some striking diversities within the group. The species may be classified into 15 behavior types with respect to periods of vegetative activity, flowering activity, and rest (Table 11).

Seven of the species have leaves which persist through the winter. Such leaves resemble the usual deciduous types, and are not to be classified with xeromorphic evergreen leaf types. They are almost entirely contained within the litter, and get additional protection from the more or less continuous covering of snow in winter.

All herbs flower between the time when the foliar buds of the trees burst, and when the leaves begin to drop in the fall. All of the tree species except basswood are anemophilous and come into flower either before the canopy begins to develop, or at the latest, before it is completely developed. Tilia blossoms about a month after the canopy is fully developed (first week in June, 1934).

Stratification. The plants of the Minnetonka Woods may be grouped into 6 strata: 1. moss, 2. low herb, 3. tall herb-low shrub, 4. tall shrub, 5. small

tree, 6. dominant tree. The moss stratum is restricted to bare areas formed by material brought to the surface by woodchucks, or exposed by windthrown trees. A group of eight species 2 to 6 inches tall constitute a scattered and poorly defined low-herb stratum. Eighty per cent of the herbaceous species attain a height of 7 to 14 inches. The distinctness of this sub-community is accentuated by the inclusion of three shrub species (Parthenocissus, Celastrus, and Rhus), which include 75 per cent of all the shrubby individuals of the forest. A separate stratum of taller shrubs is very inconspicuous. A fifth stratum of low trees includes only one species, *Ostrya virginiana*. Thus only two strata—the dominant trees and the tall herb-low shrub group—stand

TABLE 11. Periodicity of herbs, Minnetonka Woods. Explanation of symbols: L = apparently functional leaves present; F = flowering; * = no living aerial shoots, or at most very immature shoots. *Winter* is defined as: the months of severest cold (December, January and February) and most of March and April; *Spring:* interval from the time of opening of leaf buds of trees to the time when the canopy is fully developed (approximately the first three weeks of the growing season; *Summer:* period of complete canopy; *Fall:* period between the inception of leaf fall and winter.

Behavior Types	Examples	Winter	Spring	Seasons			Fall
				early	Summer mid.	late	
1. *Carex pennsylvanica, C. laxiflora latifolia, Galium triflorum, Hepatica acutiloba Ranunculus abortivus*		L	LF	L	L	L	L
2. *Osmorhiza claytoni*		L	L	LF	L	L	L
3. *Galium aparine Actaea rubra, Anemone quinquefolia, Aralia nudicaulis*		*	LF	L	*	*	*
4. *Caulophyllum thalictroides, Thalictrum dioicum, Trillium cernuum, Uvularia grandiflora, Viola pubescens*		*	LF	L	L	L	*
5. *Aquilegia canadense*		*	LF	LF	L	*	*
6. *Sanguinaria officinalis*		*	LF	L	L	L	*
7. *Aplectrum hyemale*		L	L	F	*	*	L
8. *Allium tricoccum*		*	L	F	*	*	*
9. *Arenaria latiflora, Geranium maculatum, Laportea canadensis, Polygonatum biflorum, Smilacina racemosa*		*	L	LF	L	L	L
10. *Arisaema triphyllum*		*	LF	LF	L	*	*
11. *Hydrophyllum virginianum*		*	L	LF	L	L	L
12. *Aralia racemosa, Cryptotaenia canadense, Panax quinquefolia, Sanicula gregaria, S. marilandica, Smilax herbacea*		*	*	LF	L	L	*
13. *Amphicarpa pitcheri, Circaea, Desmodium grandiflorum, Phryma leptostachya*		*	*	L	LF	L	*
14. *Solidago latifolia, Eupatorium urticaefolium*		*	*	L	L	LF	*
15. *Alliaria officinalis*		*	*	LF	LF	L	L

out distinctly. The others are exceedingly poor in species and in individuals and, further, the structure is masked by the complete series of transgressive individuals which form the reproduction of the dominant stratum.

Life forms. A classification of the species of the Minnetonka Woods according to Raunkiaer's life form system (Smith 1913) is presented in Table 12. While this scheme was originally intended for use on a larger scale, i.e. to be applied to the complete floristic list of all habitats of a region, it may also be used to advantage in comparing community types.

TABLE 12. Life form classification of the species of the Minnetonka Woods.

Size Class	No. of spp.	Percentage
Mesophanerophyte	6	10
Microphanerophyte	2	3
Nanophanerophyte	5	9
Chamaephyte	8	14
Hemicryptophyte	17	29
Geophyte	19	33
Therophyte	1	2
Totals	58	100

The community is evidently a forest dominated by mesophanerophytes, with an undergrowth composed chiefly of geophytes and hemicryptophytes.

Leaf-size classes. A classification of the vascular plants of the Minnetonka Woods, according to Raunkiaer's system of leaf size classes (Fuller and Bakke 1918) is presented in Table 13.

TABLE 13. Leaf-size classes of the vascular species of the Minnetonka Woods. (In compound leaves, the leaflet is taken as the unit; all of the plants have deciduous leaves.)

Classification		Herbs	Shrubs	Trees	Totals
Simple	Mesophyll	15	3	6	24
	Microphyll	5	2	0	7
	Nanophyll	4	0	0	4
Compound	Mesophyll	4	2	0	6
	Microphyll	11	3	0	14
	Nanophyll	3	0	0	3
Totals		42	10	6	58

Of the 58 species, 63 per cent (35) have simple leaves. Among the simple leaves, mesophylls, predominate, but in the compound-leaf group, microphylls are most important. Raunkiaer's smallest class (leptophyll) and two largest (macro- and megaphyll) are not represented in this forest. The leaves of the dominant stratum are all simple deciduous mesophylls.

Perhaps a better way of expressing the relative importance of the different leaf size classes (or life form classes either, for that matter) is by adding up the absolute densities of all species of similar leaf size. Such a summation expresses the total number of individuals, regardless of species, in each leaf size-class. This method is not floristic but physiognomic, and has more biolog-

ical significance and descriptive value than the use of simple floristic
list.   In Table 14 the scheme has been carried out for all species which
occurred in the quadrats at Lake Minnetonka; consequently, the list of species
considered is not quite so large as that used in the above table.

TABLE 14. Leaf-size classes, based on density figures of each major life form. In compound leaves, the leaflet is taken as the unit. Leaflets of compound leaves have been lumped with the simple leaves of the same size class.

Life Form	Leaf-size Class	Total Individuals per 100 sq.m.
Tree	mesophyll	2.5
Shrub	mesophyll	80.0
	microphyll	16.7
Herb	mesophyll	1129.0
	microphyll	1788.0
	nanophyll	259.0

This method gives a picture of the forest somewhat different from that
furnished by the one generally used.   According to the above table, over 80
per cent of the shrubby plants are mesophylls and comparatively few are
microphylls, but judging from the method of Table 13, mesophylls and micro-
phylls are of equal importance.   Similarly, Table 14 indicates that micro-
phyllous herbs are more numerous as individuals than are mesophyllous
herbs, which is the reverse of the condition as indicated by the simple floristic
method.

Lianas.   One herbaceous liana *(Amphicarpa pitcheri)* is moderately abun-
dant, but the species under average crown density is usually a straggling
plant.   In openings the plant climbs a few meters high.   *Menispermum can-
adense* attains a height of several meters but the parts of the stem not pro-
tected by litter are killed each winter.   The same tendency for the persisting
portions of the stem to occur chiefly under the litter and duff is shown by
Parthenocissus vitacea and *Rhus toxicodendron.*   Both of these have pros-
trate stems with upright branches about 1 dm. tall in the case of the former,
and 2 dm. in the latter.   The plants may best be characterized as potential
lianas.   On river bottoms, both climb to considerable height.   In the Big
Woods Parthenocissus sometimes climbs a meter or two, but Rhus never.
Celastrus scandens occurs as a straggling shrub under average canopy density,
but where the forest is more open, it climbs to 2 meters or more.   It fruits
only under the latter conditions.   *Vitis vulpina* is a woody liana commonly
attaining a height of several meters.

Epiphytes.   Epiphytes are poorly represented in the Big Woods.   Mosses
are common in patches on the bases of large trees.   Usually these are con-
fined to the lower 3 dm. of the trunk, but occasionally may extend up as much
as 3 meters.   A species of Porella is often mixed with the mosses around the
bases of the trees.   Crustose lichens are common on the smaller boughs near
the top of the tree canopy.

BOUNDARIES OF THE BIG WOODS

SURROUNDING VEGETATION

To the west and south of the Big Woods, the original vegetation seems to have been either bur oak savanna or tall-grass prairie. Transitions between the sugar maple-basswood forest and these communities were apparently sharp as a rule, yet instances are not rare where a distinct gradation existed from pure sugar maple-basswood through a mixture of this community with bur oak, to pure bur oak forest and savanna. Prairie and Big Woods transitions are not common, and where they exist they are always sharp.

Beginning near the northwest corner of the Big Woods and extending around the northern and eastern edges of this forest, the adjacent vegetation may be characterized as a mixed oak forest. The species involved are: *Quercus ellipsoidalis, Q. macrocarpa olivaeformis, Q. alba, Q. coccinea* (extending no farther north than Minneapolis), *Q. borealis maxima,* and *Ostrya virginiana.* The last three are much less common than the first three. *Quercus borealis maxima* and Ostrya have the most mesic requirements, and are chiefly confined to shaded slopes. Any of the three most abundant species may occur as a fairly pure stand. All sorts of combinations are found grading to a complete mixture of the entire series. This forest is obviously a more xeric community than the sugar maple-basswood; the trees are much lower, usually in open stands, and the undergrowth as a rule includes prairie herbs and shrubs.

A DETAILED MAP

A map of the exact boundaries of the Big Woods was deemed necessary, first for the clues it might suggest as to the causes of such limits themselves, and second, as a record of the original vegetational types, the indications of which are rapidly becoming effaced with the development of agriculture.

In 1873, Winchell and Peckham described the limits of the Big Woods. This account, although brief, is fairly accurate as far as it goes, and seems to be the earliest attempt to delimit this region.

More recently an attempt has been made to map the distribution of the important plant associations of Minnesota by F. J. Marshner, who has used land office records as a source of data. This unpublished map is in the possession of the Lake States Forest Experiment Station, University Farm, St. Paul, Minnesota, and the writer has made use of it to get a general idea of where to expect forest transitions in the Big Woods area.

In a number of cases, there are wide discrepancies between Marshner's map and the writer's (Fig. 3). Apparently some of the land office records are unreliable, or else difficult to interpret. It is a case of evidence based on old records vs. evidence of relic groves existing today. The latter would seem more trustworthy. For example, in a number of cases the writer found

old oak groves in regions indicated on Marshner's map as sugar maple-basswood. One can hardly doubt the reliability of an oak grove as an indicator of an original vegetational type, for oaks are seldom planted by man in this region. If they were, they would undoubtedly be set in rows; and, in any event, had they been planted immediately when the land was first claimed, they would not have had sufficient time to attain large size. Similarly, an irregularly spaced and uneven-aged group of trees belonging to the sugar maple-basswood type would hardly be found today in a region which was oak forest in comparatively recent time, except in the case of fire influence which will be discussed later.

The map was constructed as follows: County maps were used as a base, and almost all the passable roads in the region of the forest's boundaries were traversed. One person operated the car while the other recorded the forest indicators on the maps by means of convenient symbols. For the most part, sufficient indicator groves still exist to make it possible to plot the original distribution with great accuracy, but at times the lack of good indicators made the task of fixing a definite line on the maps quite difficult. The transition between sugar maple-basswood and mixed oak communities is so distinct that little difficulty was encountered in plotting this part of the boundary. The transition between sugar maple-basswood and prairie is equally as clear cut. The bur oak forest merges so gradually with the sugar maple-basswood in some places, however, that the writer has arbitrarily placed the line at a point where bur oak and the sugar maple-basswood species seem approximately equal in density.

No attempt has been made to show sugar maple-basswood areas outside of the Big Woods area. Neither has attention been paid to the occasional patches of bur oak forest which occur within the Big Woods. These, including a strip along the gravelly terraces of the Minnesota River, must owe their existence to local areas of poor soil. This inference is based on the soil studies to be later described.

The field data were transferred from the road maps to a tracing of a U. S. Geological Survey map of Minnesota. The map in final form is seen in Figure 3.

FACTORS LIMITING THE EXTENT OF THE BIG WOODS

Climate

It is generally conceded that certain phases of the moisture factor (influenced in part by temperature), acting upon the water balance of plants, exert the most potent influence in determining the distribution of the larger units of vegetation. For the state of Minnesota, Purssell's official precipitation map (1915) shows a regular decrease in total precipitation from east to west. In the latitude of the Big Woods the range is from 75 cm. at the

eastern edge of the state to less than 60 cm. at the western edge.   There is also a definite gradient in seasonal distribution, the percentage occurring during the summer months (April-October) increasing steadily to the west (Kincer, 1922)—an approach toward the type characteristic of the grassland region as a whole.

Another of Kincer's maps exhibits an additional characteristic of the precipitation gradient which is significant—the number of times when periods of drouth (defined as 30 consecutive days with less than 0.25 inches of precipitation in 24 hours) occurred between March 1 and September 30, 1895-1914. At the eastern edge of the state, such drouths occurred 18 times in the 20 years, while at the western edge they happened approximately 27 times.

Thornthwaite's (1931) map of the climates of North America constitute a more recent statement of the westward increase in xericism in this region. In the latitude of the Big Woods the western part of Minnesota is classified as subhumid and microthermal with a deficiency of precipitation at all seasons, while the eastern part is similar but has adequate precipitation at all seasons.

That climate, and especially the moisture factor, is the controlling influence in determining the western limit of the Big Woods is plainly shown by the gradual reduction of stature of the trees from east to west.   This became evident during the course of preliminary field trips, and a quantitative study of the feature was accordingly planned.   At 39 locations, well scattered over the Big Woods, measurements were made of the forest height.   Five or six representative trees in each stand were measured with a U. S. Forest Service standard hypsometer, and the average of these was taken as representing the height of the entire stand.   No trees were measured which had not to all appearances matured under closed forest conditions, and care was taken to select stands on well-drained upland, for the trees are invariably taller near streams or lakes.

When these 39 measurements are plotted on a map of the Big Woods (Fig. 4), a definite gradient is evident, the height of the forest diminishing from east to west.   The total range is from 51 to 89 feet, the former stand being near the edge of the prairie, and the latter near the eastern edge of the Big Woods.   West of an arbitrary line drawn along the longitudinal axis of the Big Woods area, the average height of the forest is 68 feet, while to the east of this line the average is 77 feet.

The fact that the trees at the western edge of the Big Woods are still almost 60 feet in height suggests that, although climate is too adverse to permit optimum development, the forest actually does not reach its climatic limit.

It was felt at the beginning of the study that it would be desirable to obtain precipitation data more directly related to the Big Woods than those available in the Weather Bureau record, and, in particular to measure evap-

oration, for which the Weather Bureau furnishes no data. The author, there-
fore, established for the measurement of precipitation and evaporation a series
of five stations extending in a line from the edge of the prairie on the west
to a point in the mixed oak forest east of the Big Woods some 52 miles distant
from the first.

The locations of the 5 stations were as follows: I, 3 miles west of Glencoe
in McLeod County; II, 2 miles north of Young America in Carver County;
III, just south of St. Bonifacius in Carver County; IV, 2 miles east of Deep
Haven in Hennepin County; and V, in Minneapolis in Hennepin County (see
Fig. 4). All stations were located in open truck gardens to obtain uniformity in
the surroundings and to insure against vandalism. Rain gauges of the type
described by Cooper (1917) were constructed by soldering a tin funnel into
the top of a kerosene can, each funnel having a vertical tin collar soldered to
its rim to prevent loss by splashing within the funnel. Approximately 200 cc.
of kerosene within the can prevented evaporation of collected rain. The
mouths of the funnels were carefully levelled at every reading. At each sta-
tion two spherical Livingston atmometers were mounted 1.5 m. above the
ground and 2 m. apart. Each atmometer was equipped with a rainproof valve,
and was standardized before and after use. An additional pair of atmometers
was kept in the Minnetonka Woods and read on the same days with the 5
stations. A comparison of the figures in the forest with those of station IV
(located 2 miles to the east in the open) gives an approximation of the in-
fluence of forest cover on evaporation at 1.5 m. above the ground, and also
serves, when compared with similar data from other parts of the deciduous
forest, as a comparative measure of the degree of mesism attained by this
community.

It was planned to take readings of the instruments at each station, at bi-
weekly intervals, during the growing seasons of 1933 and 1934. In 1933 a
serious but unavoidable break in the observations occurred, due to illness.
The data for that year have consequently been discarded. During the first
two weeks of operation in 1934, an unusually severe drouth completely dried
up all the atmometers of the transect. For this period (May 19 to June 2)
total evaporation was well over 900 cc. at all stations.

TABLE 15. Precipitation-evaporation transect of the Big Woods, June 2 to
September 22, 1934.

Station	Precipitation	Evaporation
I ..·...	19.1 c.m.	5030 cc.
II ....,.....................	22.2	4783
III ....,...................	24.2	4150
IV	20.6	4047
V	13.0	4992
Minnetonka Woods ....·........ ...		2369

The precipitation total for the summer of 1934 gives little suggestion of a gradient across the Big Woods. That a gradient exists here in both total precipitation and its seasonal distribution has been indicated by the Weather Bureau (Purssell, 1915; Kincer, 1922). It must therefore be concluded that this precipitation gradient as a whole is too slight to be detected by 4-month observations along a transect only 52 miles long.

Total evaporation for the summer of 1934 shows a definite gradient decreasing eastward across the Big Woods except for the last station in Minneapolis. This irregularity in the general trend of moisture conditions may possibly be correlated with a peculiarity in the distribution of rainfall at this end of the transect. Records of the U. S. Weather Bureau show that Minneapolis normally has somewhat less precipitation than stations a few miles west of the city, and what is even more significant in explaining the 1934 data, the anomaly was especially pronounced during this season.

POST-PLEISTOCENE HISTORY

The factors which have been of most significance in determining the distribution of vegetational types in southern Minnesota have had their origins in prehistoric time. In order to understand the relative significance of these influences, it will therefore be necessary to consider certain aspects of the history of this region since the Pleistocene epoch.

During the final stages of Late Wisconsin glaciation, central Minnesota was vegetated, at least in part (Cooper and Foot, 1932; Voss, 1934), by the boreal conifer forest. Following glaciation, rather soon according to Gleason (1922), later according to Transeau (1935), a period of warm, dry (xerothermic) climate occurred, which brought about considerable vegetational readjustment in this region. The prairie encroached upon the forested area, forcing the boreal conifer forest to retreat northward and northeastward, and the oak element of the deciduous forest increased to a maximum (Voss, 1934). After the peak of the xerothermic period had passed, the changing climate began to approach the more mesic condition of today (Gleason, 1922). Favored by this climatic trend, the deciduous forest advanced westward and northwestward, invading both conifer forest and prairie.

Such was the general sequence of events. For the region treated in this paper some special features may be pointed out. Recent studies have brought out the rather surprising fact that the soils of the Big Woods, now supporting excellent deciduous forest, possess a definite prairie profile. McMiller et al. (1934) have worked this out for the Big Woods portion of Hennepin County, and the writer's survey of the region affords ample confirmation. The evidence thus points toward the conclusion that the xerothermic period continued for sufficient time to permit development here of a typical prairie profile. Later, with the advance of the deciduous forest, the sugar maple-basswood

type took over these fine-textured prairie soils. Occupation by this community has not resulted in any significant modification of the profile. It is true that today, in the immediate vicinity, prairie is confined to the coarsest soils. Under typical grassland climate, however, with no competition from forest species, the grasses could have occupied the best soils without hindrance.

In contrast to the prairie soils of the sugar maple-basswood area, the soils to the east, supporting mixed oak forest, possess a podsolic profile. It might be assumed from this fact that these areas remained uninvaded by prairie during the xerothermic period. There is, however, the possibility that they once possessed a prairie profile which, unlike that of the finer soils, has not held its own against the influence of the invading forest.

East of the Mississippi River in Minnesota, general podsolization of fine as well as coarse soils (Cooper, 1935) suggests that the prairie invasion of the xerothermic period did not reach this region.

FIRE

The latest important climatically controlled phase in the post-glacial history of the vegetation has been the westward advance of the deciduous forest at the expense of the prairie. The actual boundary of the forest today, however, is obviously not a climatic one. The forest has, in comparatively recent time, extended farther westward, and could do so today were it not for the inhibiting effects of fire. The bulk of the damage due to this agent came through the conflagrations started by the plains Indians in connection with hunting and warfare.

The climatic limit for forest growth, at present and in past time, is, of course, a matter of conjecture. The gradient in forest height across the Big Woods is, however, suggestive. As previously mentioned, the stature of the trees decreases from nearly 80 feet at the eastern to about 60 feet at the western edge. The abrupt western edge with the trees still 60 feet tall suggests a hypothetical projection of the gradient farther westward. This leads us to infer that 100 miles west of the Big Woods the trees, if present, would be reduced to the height of shrubs. If this reasoning is valid, the present potential climatic limit of the forest is approximately 100 miles west of the present limit. It is possible that the destruction of the forest itself might have steepened the gradient of the top of the portion remaining, in which case the climatic limit would be somewhat more than the 100 miles westward assumed above.

Vegetational evidence of the influence of prairie fires in extending grassland eastward at the expense of the forest is abundant in the transition region as a whole, and follows three lines: (1) rapid natural afforestation with the development of artificial fire barriers such as roads and cultivated fields, (2) forest species persisting as relics in prairie communities, and (3) restriction

of fire-intolerant plants to the leeward of natural fire barriers such as streams, lakes, and marshes.

It has been possible to apply only one of these—the third— in the present study, the first two being unavailable because of intensive cultivation along the western and southern edges of the Big Woods. Examples of protection of vegetation by natural fire-barriers are abundant and unmistakable around the western and southern edges of the forest. A detailed map (Fig. 3) shows close correlation between the limits of the forest and such features as lakes and river valleys. At the northwestern corner the correspondence is not close enough to explain completely the limits of the forest here, but as we go southward the fires have apparently had increasingly greater influence, until in Nicollet County the forest has been almost completely eliminated on the windward side of the Minnesota River.

The behavior of sugar maple, the most fire-sensitive species, at the western edge of the Big Woods is particularly noteworthy. Here it is completely absent in those placed where fire barriers are so ineffective that they have served only to lessen the intensity of the burning. In such places a gradual transition occurs from pure sugar maple-basswood forest to bur oak savanna, and it is always the sugar maple which is the first to drop out. Red oak shows a similar behavior, and is probably the second most fire-susceptible tree.

Where fire barriers are very effective, both sugar maple and red oak are mixed with their usual associates in island-like areas well out in the prairie.

The peculiar courses of the Minnesota and Cannon rivers have apparently played a major rôle in determining the southern end of the Big Woods. Fires starting south of the Minnesota River and travelling in a general eastward direction in this latitude met the river at an acute angle which must have had little effect except to shunt them further southward along a strictly controlled course parallel to the river.[16] This deflection probably concentrated the effects of the fires as they met and followed along the river.

At the city of Mankato the Minnesota River makes a sharp turn northward, and, had not another barrier, the Cannon River, been present, the concentrated fires would no doubt from this point have come again under the direct influence of the wind and fanned out over a wedge-shaped path, increasing in width eastward.

The Cannon River is a small stream, but it meanders through a wide marshy valley cut by a glacial river during the Pleistocene. The peculiar course of this excellent fire barrier has apparently limited the lateral northward spread of the fires as far as the vicinity of Northfield. On the north side of the valley, handsome stands of sugar maple-basswood forest extend to the edge of the marsh, while on the bluffs across the valley the vegetation

[16] Grass fires in this region occur chiefly at the beginning and end of the growing season. In April the prevailing winds in southern Minnesota are from the northwest; in August and September they are divided between southwest, south, and southeast (Purssell, 1930).

is prairie with a few patches of bur oak savanna. Fires which approached the Big Woods from the south would likewise be kept entirely out of the area by the barrier formed by the Minnesota and Cannon rivers.

The gradual reduction of mesic forest to prairie through the agency of fire probably proceeded through a definite series of stages. On the east side of the Big Woods, the writer discovered an area which seems to indicate the effects of a short period of burning on the sugar maple-basswood community.

This forest is liberally sprinkled with very large bur oaks *(Q. macrocarpa olivaeformis)*, which, judging from their forms, must have developed under savanna conditions. Arising from the uppermost of the large horizontal branches are erect limbs which obviously have developed since other trees, growing up, have converted the savanna into a closed forest. The others are almost entirely Tilia and Ostrya. A conspicuous and significant feature is that the trunks of these two species usually occur in clusters.

Since this timber is in a region where one would, for climatic and edaphic reasons, expect sugar maple-basswood forest, and from the actual existing conditions as described above, the writer feels that the following interpretation is the only possible one. Repeated burning must have eliminated fire-sensitive species (Acer, if present, entirely and *Ulmus americana, U. fulva,* and *Quercus borealis maxima* partially), kept in a thicket stage those species (basswood and ironwood) whose roots remained living and produced sucker sprouts after each fire, and permitted bur oak with its thick, fire-resisting bark to develop to unusually large size due to the freedom from competition on such a favorable site. Approximately half a century ago the burning ceased, permitting the stump sprouts of Tilia and Ostrya to grow rapidly into an even-aged forest which overtopped the massive old bur oaks and caused the production of the peculiar vertical branches previously described.

Severe prairie fires, which have undoubtedly occurred for centuries, have caused still more extreme retrogression in such regions as that south of the Big Woods. Here, the sugar maple-basswood forest has been completely replaced by bur oak or even prairie. The retrogressive stages must have been similar to the following:

1. Elimination of maple from the forest (with the first burning)
2. Elimination of the elms and red oak; reduction of basswood and iron-wood to a scrub or sprout thicket
3. Replacement of sprout thicket by bur oak, and entrance of grassland herbs
4. Elimination of bur oak (with severest burning)

Summarizing briefly, the distribution of vegetation at the western and southern edges of the Big Woods indicates that these boundaries have been determined largely by the presence and configuration of fire barriers which have kept prairie fires from destroying the forest to the leeward. But for

the influence of fire, the Big Woods and its fringe of bur oak along the western edge would extend somewhat further westward, and much further southward. Evidences of fire control are less pronounced at the north end of the western boundary. In the explanation of the north and east boundaries other factors must be invoked.

SOIL

Previous mention has been made of the abruptness of the transition between the Big Woods at its eastern and northern edges and the adjacent mixed oak forest. Such a boundary is generally due either to fire, soil, or topography. This particular transition, abrupt as it is, cannot be attributed to fire, since there is no correlation between vegetation and fire barriers and because the less mesic forest lies to the leeward of the more mesic. It is therefore necessary to appeal to the other two factors—soil and topography.

Soil samples were collected from 29 stations in the Big Woods, well distributed along the northern and eastern edges, and from 29 stations just over the transition line within the mixed oak forest (see locations in Fig. 4). In each, two or three cores were collected to a depth of 3 feet. The profiles were arbitrarily subdivided so that the samples represented cores of the 0 to 6 inch, 6 to 12 inch, 12 to 24 inch and 24 to 36 inch horizons.

Approximately one-half liter of soil was collected in a paper bag for each sample. These were air-dried in a chemical-free laboratory and then passed through a 2-millimeter screen to mix the samples thoroughly and to remove skeletal material. A total of 676 samples were collected.

Each sample was tested for phosphate, pH, and moisture equivalent. Determinations of available nutrients other than phosphates would also be very desirable, but satisfactory methods of estimation have not to my knowledge been devised. It is true that a number of tests have been described, but the results of these methods usually are not substantiated by experiments in the field, which is the ultimate and final test of the significance of the method. Rost and Pinckney (1932) have applied Bray's phosphate test (1929) to Minnesota soils, and found that about 70 per cent of all experimental plots averaging "medium," "doubtful," or "low" responded to phosphate fertilizer, while only 27 per cent of those averaging "high" responded.

Available phosphate. Rost and Pinckney's work indicates that in this region at least, the critical point in the series of averages is between "medium" and "high." According to this interpretation, nearly all of the forest soils of this region were found to be well supplied with available phosphates. The differences in phosphate content of the soils on the two sides of the eastern and northern boundaries of the Big Woods is too slight to be of significance in explaining the distribution of the forest communities.

Reaction. The reaction of the samples was tested by the quinhydrone

electrode method. It is now a well established fact that air-drying of soils alters the pH values. Achromeiko (1928) found that the original pH of such dried samples can be restored if the samples are moistened 3 to 7 days before making the determinations. Bailey (1932) has more recently made an extensive study of the means which should be employed to restore the pH values of air-dried soils. His method of submerging the samples 18 to 24 hours in distilled water before testing seemed most applicable to the soils of this region, and was used in the present study. Reaction tests of the soil samples are classified in Table 6.

TABLE 16. Reaction of the forest soils as pH.

Forest Region		Depth in Inches	Total Samples	5.0–5.5	5.5–6.0	6.0–6.5	6.5–7.0	7.0–7.5	7.5–8.0	8.0–8.5
Big Woods		0–6	82	2	1	10	34	31	4	..
		6–12	82	4	16	23	23	16		..
		12–24	82	10	20	24	14	14	.	..
		24–36	81	8	25	20	10	8	9	1
Mixed Oak Forest	N. of Minn. R.	0–6	49	1	7	13	17	10	1	.
		6–12	49	..	13	14	15	5	2	..
		12–24	49	1	9	20	9	6	4	.
		24–36	49	1	7	24	3	2	8	4
	S. of Minn. R.	0–6	28	2	5	9	10	1	1	..
		6–12	28	1	13	10	2	1	1	..
		12–24	27	1	14	4	3	1	4	..
		24–36	28	1	12	2	5	1	5	2

All of these soils may be characterized as circumneutral in reaction, with a definite leaning toward the acid side. As in the case of the phosphate studies, there is too little difference between the reaction ranges of the forest types to be of significance in determining distribution.

Moisture equivalent. Moisture equivalents for the soils were determined by the Briggs and McLane (1907) method. With each group of samples simultaneously centrifuged, a pair of check samples of known moisture equivalent was included. Whenever the results from the latter varied from their true percentages, the unknowns were again tested until their checks gave the correct values (Table 19).

Along the northern and eastern edges of the Big Woods there is a difference in the water-holding power of the soils of the two forest types in the portion north of the Minnesota River, but south of this point there is very little difference in this respect between sugar maple-basswood and oak forest soils. It will be most convenient to discuss the two parts of the transition line separately.

North of the Minnesota River, most of the oak forest subsoil samples are

TABLE 17. Moisture equivalents of the forest soils. The modal classes of the horizontal arrays are italicized.

Forest Region		Depth in Inches	Total Samples	Moisture Equivalent Per Cent Classes									
				0-4	4-8	8-12	12-16	16-20	20-24	24-28	28-32	32-36	36-40
Big Woods............		0-6	83	..		1	11	*24*	22	16	8	1	..
		6-12	83	..		8	*30*	21	17	7	..	..	..
		12-24	83	.		8	23	17	*24*	8	3	.	..
		24-36	82		5	6	16	14	*20*	14	6	1	..
		0-6	49	.	10	8	12	*16*	2	..	1	..	..
Mixed Oak Forest	N. of Minn. River	6-12	49	4	*18*	8	9	7	3	..		..	..
		12-24	49	11	*18*	7	5	2	4	2	..	.	..
		24-36	49	*18*	14	3	7	2	3	2	..	..	
	S. of Minn. River	0-6	34	..	..	2	7	8	*9*	3	2	2	1
		6-12	34	..	.	3	*12*	7	5	4	3	..	..
		12-24	34	..		5	4	*11*	8	4	1	1	..
		24-36	34	..	1	4	9	4	9	4	1	..	2

coarser (assuming the moisture equivalent to be an indicator of texture) than any encountered in the Big Woods. Two factors might be offered to explain the relatively few cases where the moisture equivalent ranges of the two regions overlap. Since the soils of this region are derived from several layers of glacial drift varying widely in thickness, original nature, and amount of modification, it is quite natural that local areas of fine-textured drift should occur as island-like masses in the coarser materials, which, because of insufficient lateral or vertical extent would be rendered unfavorable by the excessive drainage incurred by the surrounding coarse soil. Again, the overlapping of texture ranges was favored by the locations of the soil stations, for Big Woods and oak forest soils were both collected very near the transition line (sometimes less than ½ mile apart) where a minimum of difference between the two forest soils would be expected.

All of the Big Woods occurs on thick Young Gray Drift of Late Wisconsin age. North of the Minnesota River the edge of the Big Woods corresponds closely with a rather abrupt thinning of this drift. The mixed oak forest soils have been derived from either older, coarse Red Drift of mid-Wisconsin age, with a thin layer of Gray Drift over the surface, or else outwash material derived from both parent bodies. This correlation between the forest transition and the abrupt thinning of the Young Gray Drift seems causal.

The region where soil texture seems to be important begins on the east side of the Big Woods at the Minnesota River and extends northward around the north end and down the west side to central Meeker County. Beyond this point no samples were taken for two reasons: (1) south of here the lim-

its of the Big Woods begin to show more constant correlation with fire-barriers, and (2) *Quercus ellipsoidalis* extends rather conspicuously around the Big Woods to this point, beyond which bur oak is practically the only species in the narrow strip of forest between the sugar maple-basswood community and prairie. Since the fire-sensitive *Quercus ellipsoidalis* is absent, and the dependence of the Big Woods limits on fire barriers becomes very conspicuous, it was concluded that southward from central Meeker County, the primary factor limiting the Big Woods was fire.

The writer has as yet little to offer in explanation of the transition from sugar maple-basswood to mixed oak forest along the portion of the east boundary between the Minnesota River and Northfield. Analyses of the soils on the two sides of the line are very similar; the position of the oak forest to the leeward of the Big Woods and the abundance of *Quercus ellipsoidalis* preclude the possibility of fire influence.

There is, however, a definite difference in topography. The region to the west of the line is extremely hilly, being a part of the pronounced subterminal moraine of the Young Gray Drift. To the west of this boundary is an undulating till plain of the same kind of drift. The region of the terminal moraine seems to have a low water table, for the depressions between the knobs seldom contain lakes, and in this respect differs strikingly from the lake-dotted till plain. I venture the suggestion that the low water table may have prevented the establishment of the mesic type of forest on the uplands. Ravines in this region are heavily wooded with sugar maple-basswood forest, but this is hardly significant since the same holds for practically all ravines of any size in central Minnesota. Beyond this moraine to the, east are entirely different types of parent material (outwash, Kansas drift, or Young Red Drift) all of which are characterized by a narrow zone of mixed oak forest beyond which is fire-induced prairie.

In summarizing these soil studies, there seems to be no relationship between soil reaction or available phosphate content and the distribution of forest types in this region. A part of the eastern, and the northern limits of the Big Woods, corresponds closely to the edge of the unmodified Late Wisconsin drift; the soils beyond this edge have a much lower water-holding capacity as a rule. South of the Minnesota River the Big Woods ends at the edge of a moraine, the soils of which seem favorable to sugar maple-basswood forest, according to the analyses. A low water table or some other condition accompanying the moraine has here inhibited the more mesic forest from the uplands.

DISTRIBUTION OF THE SUGAR MAPLE-BASSWOOD CLIMAX

The northwest portion of the deciduous forest seems to be a complex of closely related communities, with nearly the same list of dominants, and typified by the sugar maple-basswood climax.

On the White Earth Indian Reservation in northern Minnesota, Ewing (1924) has described the climax community of the deciduous forest belt as consisting of *Tilia americana, Ulmus americana, Acer saccharum, Fraxinus pennsylvanica lanceolata, Populus tremuloides,* and *P. balsamifera.* The relative importance of the species in the above list is not discussed.

About 22 miles east of this reservation, Lee (1924) has studied the forest successions around Lake Itasca in Clearwater County, Minnesota. He describes a sugar maple-white pine type as one of four virgin communities. This occupies the fertile clay soils, while others are limited to sandy or swampy sites. The important species are *Acer saccharum, Pinus strobus, Tilia americana, Ulmus americana, Quercus borealis* or *Q. borealis maxima, Q. macrocarpa (=Q. macrocarpa olivaeformis),* and *Betula papyrifera.* In this community, white pine owes its existence to local openings in the stand.

Approximately 30 miles east-northeast of Lake Itasca, Kittredge (1934) has described a forest succession on sandy outwash on Star Island in Cass Lake, near the southeast corner of Beltrami County, Minnesota. In this series sugar maple-basswood is climax. The trees, listed in order of importance, are *Acer saccharum, Tilia americana, Ulmus americana, Quercus borealis,* and *Ostrya virginiana.* Basswood has a higher density than sugar maple, but this is attributed to fires in the past. Abundant reproduction of the maple seems to indicate that if undisturbed it becomes most important.

East of the Star Island region, the forest climax of the better soils seems to be a hybrid type of community containing dominants from both the boreal conifer forest and the sugar maple-basswood community. Grant (1934), working in Itasca County, Minnesota, lists the climax species in order of importance as follows: *Abies balsamea, Tilia americana, Quercus borealis maxima* and *Q. borealis, Betula lutea, Picea glauca, Ostrya virginiana.* He states that this is "probably the climax community over most of the coniferous forest region of Minnesota, except in the extreme northeastern corner of the state." Judging from the studies by Ewing, Lee, and Kittredge mentioned above, the type described by Grant does not extend west of Itasca County. From Itasca County eastward, sugar maple occurs chiefly along lake margins where, according to Rosendahl and Butters (1928) it is protected from unseasonable frosts. The tree reproduces poorly in this northeastern region.

In upper Michigan, the deciduous forest may be divided into several types, one of which is very similar to the Big Woods. Westveld (1933) has studied the composition of these forest communities in the northern peninsula. Here the deciduous forest is found only on loam soils; coarse soils have pines, and

finer ones mixed swamp-conifer and deciduous species. The composition of
two stands of sugar maple-basswood in this region, expressed as density per-
centage of trees 0.5 inch d.b.h and over, is given as follows:

	On Stambaugh silt loam Per cent	On Iron River silt loam Per cent
Acer saccharum	75.8	63.8
Tilia americana	10.9	10.1
Ostrya virginiana	4.9	3.9
Betula lutea	0.5	7.1
Abies balsamea	1.6	6.2
Tsuga canadensis	1.4	5.4
Ulmus americana	1.4	2.7
Prunus serotina	3.4	0.0
Picea glauca	0.4	0.0
Thuja occidentalis	0.3	0.0

McIntire (1931) gives the composition (expressed as basal area in sq. ft.
per 1,000 sq. m.) of a stand of sugar maple-basswood on Trenary loam in
Alger County, northern Michigan:

Acer saccharum	27.63
Tilia americana	3.34
Ulmus	2.73
Betula lutea	1.06
Others	.82
Total	35.22

In lower Michigan, the climax forest of better soils is dominated by *Acer
saccharum, Fagus grandifolia, Tilia americana, Tsuga canadensis, Betula
lutea* and others (Quick, 1923). On the west side of Lake Michigan, Fagus
is first to drop out of the climax forest (see list of species by Zon and Scholz,
1929), and next Tsuga and Betula. Tilia, increasing in relative importance
from New England westward (Frothingham, 1915), becomes second to Acer
beyond the region where Tsuga and Betula are important.

Sugar maple-basswood forest also occurs in Illinois. Gleason (1912) con-
siders the "hard maple-basswood type of forest" as "the highest type found
in central Illinois."

Aikman has described the climax forest community in Iowa (1930) and
along the eastern edge of Nebraska (1926) as a red oak-basswood association.
In Nebraska the most important trees, in order of importance, are *Tilia
americana, Quercus borealis maxima,* and *Ostrya virginiana,* while among the
others are *Carya cordiformis, Fraxinus pennsylvanica, Ulmus americana,* and
U. fulva.

Generalizing from the published accounts reviewed above and from the
present study, it seems that the sugar maple-basswood type is the regional
climax of the northwest corner of the deciduous forest, in Minnesota, prob-

ably much of Wisconsin, and central Illinois. Approaching the boreal conifer forest, the sugar maple is reduced to a minor rôle and a transitional climax dominated by balsam fir and basswood is characteristic. Approaching Lake Michigan and the main body of the deciduous forest to the east, basswood becomes reduced in relative importance, and hemlock, yellow birch and beech accompany sugar maple as important dominants. Toward the prairie to the south and west, sugar maple drops out of the community leaving basswood, red oak, and ironwood as the chief dominants of a closely related community.

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THE AGGREGATION BEHAVIOR OF *STORERIA DEKAYI* AND OTHER SNAKES, WITH ESPE-CIAL REFERENCE TO THE SENSE ORGANS INVOLVED

By

G. K. NOBLE and H. J. CLAUSEN

Department of Experimental Biology, American Museum of Natural History

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THE AGGREGATION BEHAVIOR OF *STORERIA DEKAYI* AND OTHER SNAKES, WITH ESPECIAL REFERENCE TO THE SENSE ORGANS INVOLVED

INTRODUCTION

It is often assumed that snakes show no social behavior except during breeding season and at times of hibernation (Prater, 1933). However, if large numbers of certain species are frightened while in an exposed situation they come together to form compact masses. In the case of the common brown snake, *Storeria dekayi,* the individuals entwine themselves into a large cluster and the entire group can be picked up by taking hold of only a portion of the mass. Other species, such as *Thamnophis butleri,* do not react to the same degree and the resulting masses are consequently not as compact. The tendency to form these masses in exposed situations after frightening is found in both the young and mature individuals regardless of the period of the year.

Aggregation as the result of disturbance probably rarely occurs in nature because there are usually sufficient means for retreat. There is, however, another type of response which doubtlessly occurs frequently in nature and has also been noted under laboratory conditions, namely aggregation when environmental conditions are unsuitable.

Although *Storeria dekayi* and *Thamnophis butleri* are as well known as most North American snakes the tendency of these species to aggregate under the above conditions has not been previously described. The aggregation behavior of animals has recently been critically reviewed (Allee, 1931). Our knowledge of the mechanism of aggregation in vertebrates higher than fishes is very poorly known. Hence it has seemed desirable to analyze the behavior in the snakes available to us in series. The recent works of Baumann (1929), Kahmann (1932) and Wiedemann (1932) have thrown new light on the rôle of the sense organs in the feeding reactions of serpents. In view of these studies it has seemed desirable to make some comparison between the feeding and aggregating behavior of the species utilized in the present study.

THE FORMATION OF AGGREGATIONS IN *STORERIA DEKAYI*

The compact aggregations of *Storeria* as above described may be readily induced in groups of individuals at temperatures between 18° and 26° C. by removing all covering from the floor of the cage and then jostling the cage. The response is also in evidence when certain environmental conditions are altered. If large numbers of *S. dekayi* are left undisturbed in large cages containing sand and moss of various degrees of dampness they will usually

be found in clusters of about 10 to 15 individuals. Most of these clusters are found between the drier and damper layers of moss. If these layers are disturbed the clusters will break up into approximately 4 to 5 individuals in a group. It may be assumed that these aggregations which form in the absence of any disturbance are due to snakes, coming together in regions of optimum conditions of humidity and temperature. Nevertheless, when humidity conditions throughout the mass are equalized or the sand uniformly dampened, the snakes still come together to form clusters. A study of a large series of individuals under a wide range of humidities and temperatures made it clear that *S. dekayi* exhibits a well marked tendency to aggregate with others of its own species and also that this tendency becomes more marked by disturbing or irritating factors.

AGGREGATIONS IN THE FIELD

It has not been previously recognized that *Storeria dekayi* forms well marked aggregations in the field at all times of the year. Records were made of the degree of aggregation in a large series of individuals collected outside the breeding season at Flushing, N. Y. Excluding the gestating females, which do not aggregate, we found the other 497 snakes distributed as follows:

Isolated 184	Aggregated 313										
	In groups of......	2	3	4	5	6	7	8	9	10	11	12
	Number of Snakes.	112	66	48	35	18	14	8	..	..	..	12

In other words, no less than 63 per cent of all the snakes observed outside of the hibernating season and excluding the gestating females, are found aggregated and usually in small groups. Most of these snakes were found under pieces of wood, paper or other detritus. We have included in the above figures only those snakes which were in actual contact. If we should consider all snakes under the same object to be aggregated, the total number of aggregated snakes would exceed 79 per cent. Moreover, 74 per cent of the 497 individuals were found in two areas each approximately 30 ft. square. DeKay snakes were collected at other times and other places. The size of the aggregated groups and the spotty distribution were very similar to that studied in detail in these 2 areas. It will be shown below that the clustering under the same object or within the confines of a limited area may also be considered a manifestation of the aggregation drive.

The most extensive aggregations of *S. dekayi* are those of hibernation. In the fall of 1932, Mr. S. C. Yeaton found the first hibernation den on a small knoll on the edge of a swamp on the outskirts of Flushing, N. Y. The den was apparently an old rat burrow which faced south. Although the burrow

was only 11 inches deep no less than 76 *S. dekayi*, 10 immature *T. sirtalis* and 1 immature *Natrix sipedon* were taken from the bottom of the single chamber which ended blindly. So far as we are aware this is the first time a hibernating den of *S. dekayi* has been reported. The fact that this species may hibernate with a species with which it does not ordinarily associate during the greater part of the year is of considerable interest and will be again considered in a later part of the report.

This series of *S. dekayi* taken in hibernation, ranged from 110 to 325 mm. in total length on February 14, 1933. When the total lengths of all the individuals in the series were plotted it was found that there were 2 distinct modes with one mean at 155 mm. and the other at 271 mm. There were 56 snakes in the mode having the smaller mean and 24 in the other. No individuals fell in the range between 210 and 230 mm. When the sexes were plotted separately no well defined difference was noted in the curve. The young of *S. dekayi* have been reported in one case to range from 102 to 110 mm. at birth on August 13 (Force, 1930) and in another case, to range from 100 to 107 mm. shortly after birth on August 17 (Shields, 1929). One *S. dekayi* collected in November 1933 and kept in our laboratory, gave birth to 5 young, 3 of which were still-born, on March 20, 1934. The female was 310 mm. in length with the largest young measuring 80 mm. and the average of the 5 being 78 mm. It is apparent that the individuals in our smaller mode were young of the first year. Since *Storeria* breeds normally in the early spring, the individuals in our smaller mode would obviously not breed the first year of their life. Adult size is apparently obtained, however, by the following fall and hence sexual maturity is presumably reached by the second spring in the life of the species. Direct proof of this contention is afforded by the data presented in Table 1. A snake (103) collected, marked and released in the field October 31, 1933, was 190 mm. in total length. By December 8, 1934, it had grown to 300 mm. in total length. Six other young snakes (Nos. 10, 20, 3, 127, 50 and 119) added over a hundred millimeters to their length between October or November of one year and December of the following year. Only one young snake (No. 80) which lived under natural conditions for over a year failed to add a hundred millimeters to its length.

During the past 2 years of field study over 500 *S. dekayi* were collected and brought into the laboratory and 186 others were marked by cutting off one or more of the subcaudal scales (according to the method of Blanchard and Finster, 1933). These marked snakes were released again so that normal movements and migrations could be further studied. The snakes were found under small pieces of paper, tin, tarpaper and, less often, under stones. They were also found actively crawling around in the grass at different times of the day. The favorable localities were on slopes with southern exposures. In the region where *Storeria* occurred, they were usually observed in groups.

TABLE 1. *Storeria dekayi* found in Den B on December 8, 1934.

Snake No.	Sex	Size in mm.	Original Location	Date Found	Migration Distance to Den	Size in mm. When Found in Den
103......	♂	190	Region A	10–31–33	60 yds.	300
175......	♀	490	Region C	3–22–34	....	490*
10......	♀	180	Region D	10–26 -33	450 yds.	310†
80......	♂	200	Region C	10–30–33	1320 yds.	295
4......	♂	315	Region C	10–26–33	1320 yds.	315
20......	♀	220	Region B	10–26–33	....	326
3......	♂	182	Region C	10–26–33	1320 yds.	283
127......	♂	194	Region B	11– 5–33	....	314
15......	♀	315	Region B	10–26–33	....	315
50......	♂	177	Region B	10–27–33	....	323
119......	♀	208	Region B	11– 3–33	....	346

*Found in C, but placed in B, 3-22-34. Therefore no migration.
†D region is located west of B region between B and C.

For example, on one southern slope (Fig. 1) only 2 areas, each approximately 10 feet square, were ever inhabited. One of these areas is in the immediate foreground in Figure 1, while the other is 50 yards west in the background of the above figure. The intervening territory between these 2 areas never yielded any snakes. These 2 regions will be designated as regions A and B in the following discussion. The slope was examined at 2 to 3 day intervals for a period of 3 months. Some of the snakes were brought back to the laboratory for further study; the marked individuals were released where they were originally found or in some instances they were released some distance away. The marked snakes usually remained in the region where they were released providing they were originally found there. However, if they were released in a locality some distance from where they were found, they often returned to the original location. That is, of the 32 snakes marked and released in a foreign territory, 13 of them returned to the original spot over a 70-day period. In other words, about 40 per cent of this group returned to their original locality. The average distance this group moved in a period of 3 days was between 10 and 15 feet. However, our records show that out of the group of 32 snakes, 8 had each migrated nearly 1,320 yards in the period of one week. The return of the above 40 per cent to their original locality leads to the question of whether the movement was a true homing, or was due to a random movement and the accidental termination at the original point where conditions might have been especially favorable.

Occasional, observations continued until November 18, 1933, when no snakes were found in any of the favorable regions. The air temperature at this time was 7° C. Since no snakes were to be found on the surface of the ground at this time, region B, an area 10 x 15 feet, where *S. dekayi* had always been found in large numbers, was examined for rat burrows. No

Fig. 1.   The habitat of *Storeria dekayi*.   Two areas, each approximately 10 feet square were the only sections of this southern slope which were inhabited by the species.   One area is in the immediate foreground while the other is 50 yards west, in the background of the picture.


Fig. 2.   A part of a hibernating den where *S. dekayi* were found.   The ground is undermined, as shown, with ant tunnels in which the snakes were found.

snakes were found in any of the burrows in this or the surrounding area. An excavation was made approximately 3 feet square and 3 feet deep. In this excavation, in small underground channels apparently made by ants, 62 DeKay snakes were found in clusters of 2 or 3 and in a few cases as many as 6. The ground throughout this area was found to be undermined with these tunnels which were approximately 0.5 inch in diameter (Fig. 2). *Storeria* were found in this excavation from a depth of 6 inches to 2.5 feet from the surface. The ground was very dry at the latter depth and at a depth of 3 feet the channels or tunnels were inhabited with black ants *(Formica subsericea)*.

On March 20, 1934, the first *S. dekayi* were found since the previous fall. These snakes were again found in the exact region where a large number of snakes had been collected the previous year. This region is designated region C and was located approximately 1,320 yards west of region B. A small rock was found in region C and underneath it a hole, 0.5 inch in diameter, was found which led down vertically to a depth of 2 feet and branched horizontally in two opposite directions. At this depth the sandy soil was mixed with small pieces of rock and tin and had no doubt been filled in some years previous. In these channels and crevices, 45 *S. dekayi* were found in groups of 2 or 3 up to 10 in a cluster. Between the groups of *Storeria* there were several groups of *T. sirtalis*. The snakes were grouped irrespective of sex. Fifteen *T. sirtalis* were removed and in no case were any of them in contact with the *S. dekayi*. Of the 45 DeKays only 10 were snakes which had been marked and released the previous year. These 10 snakes had been released within a radius of 45 feet from the hibernating den. All new *S. dekayi* found in this den were marked and released in regions A and B for further study during the summer.

Up to this time (March, 1934) 186 *S. dekayi* had been marked and released. The regions where all of these individuals had been placed as well as the surrounding territory were carefully examined at intervals of 2 or 3 times per month for the period from April to December. During the months of April to October only 5 of the marked snakes were found again and the distance they had migrated since being marked varied from 12 to 1,320 feet. It is of interest to note that these snakes were at a distance from the regions they had inhabited during the spring or the previous fall. Six marked individuals found during the months of October and November had returned to their original place of hibernation. From these observations it may be concluded that during the summer and early fall months DeKay snakes move about at random. During the months of October and November there is a migration toward the hibernation regions. The region or den selected may or may not be the same one utilized the previous year.

On December 10, 1934, the hibernating den in region A was again exca-
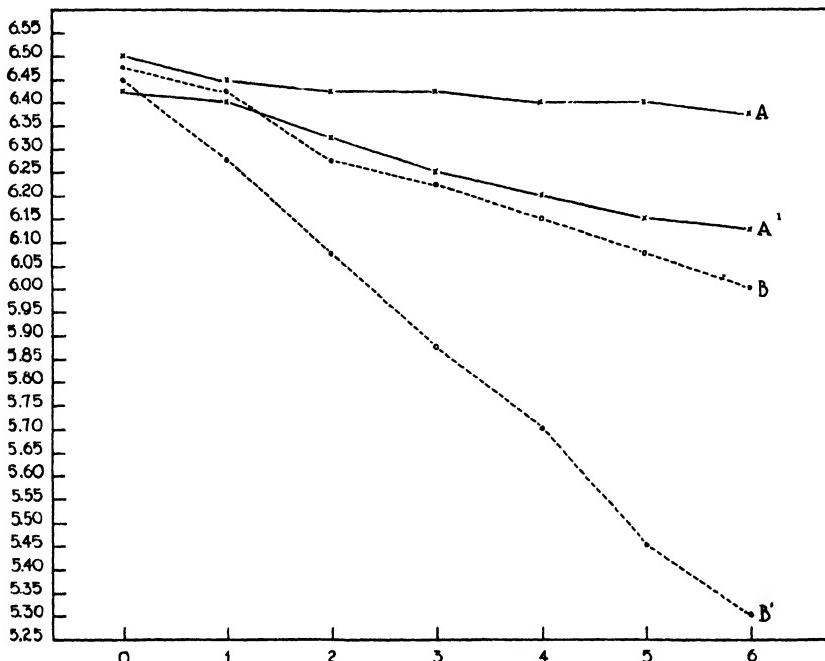
FIG. 3. The average loss in weight of five *S. dekayi* in both the isolated and aggregated condition over a period of 6 hours at constant temperatures. Abscissas, hourly periods; ordinates, average weight in grams; continuous lines A and A¹, decrease in weight of aggregated snakes at 30 and 35° C. respectively; broken lines B and B¹, isolated snakes at 30 and 35° C, respectively.

vated. Ninety-seven *S. dekayi* were found in the ant tunnels as previously described. Of this group only 11 were individuals that had been marked. Five were found here originally and released here within 10 to 15 feet from the den. The other 6 individuals had been found elsewhere and placed here (Table 1). From this table it would seem that snakes 20, 127, 15, 50 and 119, having been found in the original location after being released more than a year previous, had returned to their original hibernating den. Since they were not found in this location during the intervening time they had presumably moved away and then returned. But these snakes were all released in 1933 and they were not found in this den area when it was excavated November 18, 1933. It is possible they were overlooked in some channel not completely excavated but it is more probable that they hibernated elsewhere the first winter. From these data it may be concluded that snakes do not necessarily return to the same den year after year. DeKay snakes migrate to a region most suitable for hibernation and this region may or may not be the same den utilized in previous years. This is well shown by the movements of snake No. 175 (Table 1), an individual removed from a den in region C in March and placed in region B at that time. The snake was

found hibernating in region B the following year. No evidence of an attempt to return to region C was disclosed. The remaining snakes as recorded, showed evidence of migration toward the den in region B even though they were originally found in other regions. The latter regions were near other hibernating dens to which these snakes might have returned.

During the months of June and July no aggregates were found in the hibernating or surrounding areas. The adult male snakes and half grown individuals were always found in the open and actively crawling around while the adult females were always found isolated under stones or paper where the ground and dead grass were moist. These females go into seclusion during the last part of the gestating period and remain in one locality until parturition. Six gravid females were found during the last week in June and were observed to remain in exactly the same spot till the last week in July when the young were born. In no case was there evidence that the female had left the rock or paper at any time during this period, since observations were made frequently and notes made of their position under the rocks or paper.

From our field observations on *S. dekayi* it may be concluded that aggregation occurs at all times of the year except, in the case of adult females, during the months of June and July. At this time such females are gestating and isolated from the males or other females. The aggregations found in the ant tunnels or other subterranean channels of the den areas in mid-winter are of course more concentrated than the scattered aggregations of mid-summer, but the mechanism which produces both types of grouping is, we believe, essentially the same. In order to elucidate the various sensory components involved in these aggregations we have performed a series of experiments which will be described below.

Laboratory Care of *Storeria*

A total of 400 *S. dekayi* was collected from these various regions during the past year and brought to the laboratory. They were placed in wood frame cages measuring 21 x 15 x 14 cm. and having glass sides and a screened top. On the tin bottom of the cage 2 cm. of gravel were spread out and 2 or 3 thicknesses of moss were then placed over the gravel. One layer of the moss was always kept moist. A dish of water and a supply of larvae of the meal beetle *(Tenebrio molitor)* and of the wax moth *(Galleria mellonella)* were always kept in the cages. Earthworms were placed in the damp layer of moss from time to time. The water in the cages was changed daily.

A series of *T. butleri* employed for comparison in these studies was composed entirely of adult snakes collected from the vicinity of Olean, N. Y. The smaller series of *T. sirtalis* and *T. sauritus* were taken from several local-
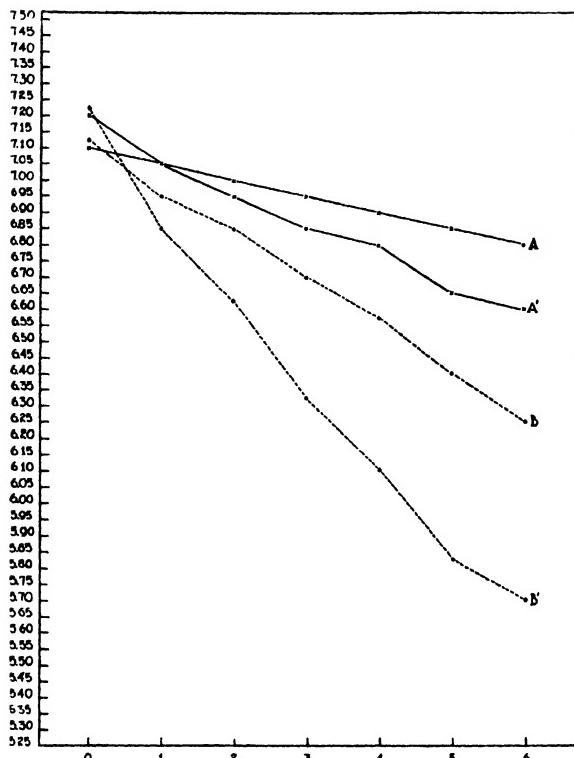
FIG. 4. The average loss in weight of five *T. butleri* in both the isolated and aggregated condition over a period of 6 hours at constant temperatures. Abscissas, hourly periods; ordinates, average weight in grams; continuous lines A and A¹, decrease in weight of the aggregated snakes at 30 and 35° C. respectively; broken lines B and B¹, isolated snakes at 30 and 35° C. respectively.

ities in New York State and covered a wide range of age groups. Throughout the work we have noticed no consistent differences in the aggregation response between the sexes or between the different age groups.

RATE OF EVAPORATION DURING ISOLATION AND AGGREGATION

If external environmental factors are primarily responsible for aggregation then the physiological state of the snake must in some way be affected by these changes. A series of experiments was carried out to test several physiological factors which are involved in this grouping response. In this series a comparison between isolated and aggregated *S. dekayi* and *T. butleri* was made over a 6-hour period at temperatures of 30 and 35° C. and relative humidity at 25 per cent, to note the amount of water loss in both species in both the aggregated and isolated condition. The changes in body weight were

used as a criterion in determining the loss of water. An isolated snake was placed in one box while a group of snakes was placed in another box. The boxes in both cases were of equal size, being made of wood and measuring 14 x 11 x 6 cm. and fitted with a sliding cover. The boxes were weighed before and after placing the snake or snakes into them. After recording the above weights the boxes containing both the isolated and the grouped snakes were placed in a constant temperature chamber. The snakes that were used as experimentals had not been fed for 1 week previous to the experiment so as to eliminate as nearly as possible any weight loss due to excretion. The isolated animals used in the tests were also employed as individuals of an aggregate so as to eliminate individual differences. At intervals of one hour each, up to and including the sixth hour after placing the snakes in the constant temperature chamber, the boxes were removed and weighed again both with and without the snakes in them and the snakes were also weighed again by placing them in small paper boxes on an analytical balance. This method of weighing therefore checked the weights of the snakes as well as the containers each successive hour during the experiment. Figure 3 records the average weight in grams of 5 *S. dekayi* over a 6-hour period at temperatures of 30 and 35° C. in both the isolated and aggregated condition. The average loss in body weight in the isolated condition during the 6-hour period was 7 and 17 per cent respectively at temperatures of 30 and 35° C. The aggregated snakes showed a loss of 1.5 and 4.5 per cent per individual over the same period at respective temperatures of 30 and 35° C. Figure 4 records a comparative series of experiments similar to the above but carried out with *T. butleri*. With this species the loss in weight for isolated individuals was 10 to 20 per cent at respective temperatures of 30 and 35° C. and for the aggregated cases 4.2 and 8.3 per cent respectively at the above temperatures. Hence, under similar conditions of temperature and humidity, *S. dekayi* becomes desiccated less rapidly than does *T. butleri*, whether isolated or aggregated.

The results of these tests show that aggregation is beneficial in that it conserves water. As the temperature increases, the result of this grouping phenomenon becomes more and more beneficial. There is a marked difference between the water loss of various species. Since *S. dekayi* is a smaller species than *T. butleri*, a group of individuals of the first species having the same weight as a group of the second should lose more water if the permeability of the skin to water were the same in both forms. The fact that such a group of *S. dekayi* loses less water may be considered an adaptation to the drier habitats occupied by this species. The case is similar to that in lizards where the species living in dry habitats have been found to lose less water through their skin than those frequenting more moist situations (Noble and Mason, 1933).
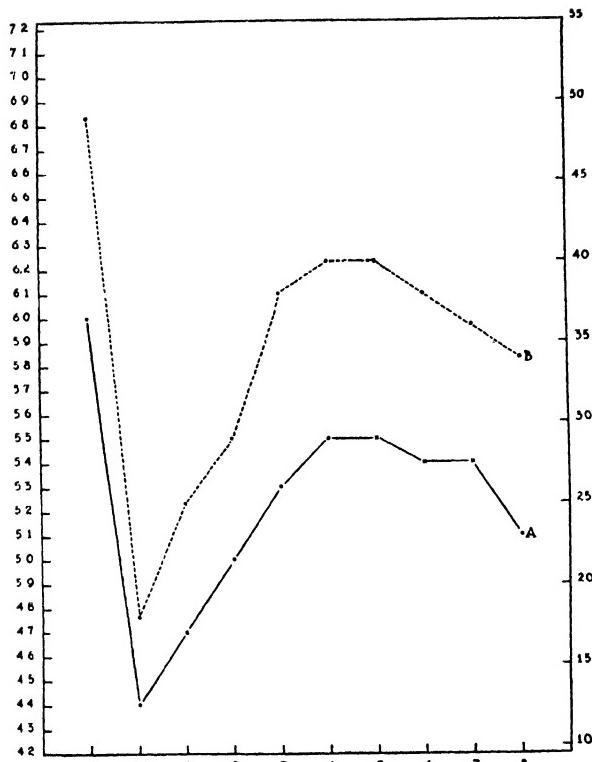
F IG . 5.   Correlation between respiration rate and
weight loss over a period of 32 hours at a temperature of
30° C. for five isolated *S. dekayi*. Abscissas, 1-24, hours
in a dry container and remaining 8 hours in a moist con-
tainer.   Ordinates: left, weight in grams; right, respir-
atory rate.   The continuous line A, weight; broken line
B, respiratory rate.

E FFECT OF A GGREGATION ON R ESPIRATION

Since aggregation so obviously reduces water loss it presumably influences
other metabolic activities such as respiration.   The effect of aggregation on
the rate of respiration was determined by observing the thoracic or abdom-
inal movement in a group of *S. dekayi* in both the isolated and aggregated
condition over a 6-hour period.   The snakes, either isolated or in groups of
five, were placed in small wood boxes of the same size as used in determining
the water content in the previous experiment.   These boxes were then placed
in a constant humidity and temperature chamber.   Throughout the experi-
ment the temperature was kept at 25° C. and the relative humidity at 40 per
cent.   Table 2 records the average changes in rate of respiration of the same
5 isolated and 5 aggregated *S. dekayi* over a 6-hour period.

It is shown in the table that soon after *S. dekayi* aggregate their rate of

respiration is decreased. With time the decrease continues, but in both isolated and aggregated snakes if the aggregates and the isolated individuals are compared after a 6-hour period the snakes in the aggregate are respiring more rapidly than the isolated ones. Both the isolated and the aggregated groups have come to have lower rates than at the beginning of the experiment, but the decrease is much greater in the isolated series. The decrease in the isolated series is correlated with the greater loss of water. In an earlier series of experiments it was shown that aggregations lose water less rapidly than isolated individuals and in connection with the above studies a series of tests was made to show that aggregations also take up water less readily than do isolated snakes when placed in a moist environment. This series also shows that the respiratory rate is in direct correlation with the water content of the body.

The methods for determining the water intake in the isolated and grouped *S. dekayi* were essentially the same as those used for the water loss determinations except that a lining of moist blotting paper was introduced into the small boxes. The snakes were placed in the small wood boxes, the isolated in one and the aggregate of 3 snakes in the other box. These boxes were placed in the constant temperature chamber at 30° C. and left for 24 hours, at which time they were removed and the respiratory rate and weight of each snake were recorded and compared with the original record. The blotting paper lining the boxes was moistened with 5 cc. of water. The weight of the box was then recorded and the isolated and aggregated snakes placed in their respective boxes which were then replaced in the constant temperature chamber. At intervals of one hour thereafter, the aggregate of 3 snakes as well as the isolated snake was removed, the respiratory rates and weights of each individual recorded and the animals again replaced in the boxes in the temperature chamber. Hourly records were made for a period of 8 hours to correlate the relationship between water intake and respiration. This series of experiments was repeated 5 times with different snakes in the aggregated and isolated conditions and also with the same individuals in the same situations. Figures 5 and 6 record the averages for the isolated and aggregated individuals respectively. These graphs show the loss of weight is correlated with a decrease in respiration. Desiccation tends to reduce both the weight and the respiratory rate. A direct correlation also exists between the increase in weight and the increase in respiration in both the isolated and aggregated series.

It will be noted that the respiratory rate of the isolated snakes is at first very much higher than that of the aggregated individuals but it drops below that of the latter during the 24-hour period. As stated above, the initial high rate is apparently due to the excitement and activity of the isolated individuals. If the isolated snakes are kept moist their respiratory rate will not drop be-

TABLE 2. Comparative respiratory rates of aggregated and isolated *Storeria*.

Case	Size (mm.)	Resp. Count (3 tests) 1	2	3	Average Count	Grouped or Isolated Time
1............	255	60	65	60	61.7	Isolated 1 hour
		60	58	62	60.0	" 2 hours
		40	35	42	39.0	" 4 "
		20	18	25	21.0	" 5 "
		10	12	10	10.6	" 6 "
2............	305	57	60	55	57.3	Isolated 1 hour
		64	60	62	62.0	" 2 hours
		43	41	38	40.6	" 3 "
		30	35	33	32.6	" 4 "
		25	30	23	26.0	" 5 "
		15	12	15	14.0	" 6 "
3............	290	50	56	54	53.3	Isolated 1 hour
		40	47	44	43.6	" 2 hours
		40	45	40	41.6	" 3 "
		25	18	23	22.0	" 5 "
		20	20	15	18.3	" 6 "
4............	250	55	58	50	54.3	Isolated 1 hour
		50	48	51	53.0	" 2 hours
		40	45	42	42.3	" 3 "
		20	26	23	23.0	" 5 "
		18	20	20	19.3	" 6 "
5............	205	28	35	30	31.0	Grouped 1 hour
		30	32	30	30.6	" 2 hours
		26	28	28	27.3	" 4 "
		27	25	26	26.0	" 5 "
		25	25	26	25.3	" 6 "
6............	255	34	35	35	34.6	Grouped 1 hour
		30	30	30	30.0	" 2 hours
		25	26	25	25.3	" 4 "
		25	25	25	25.0	" 5 "
		24	25	25	24.6	" 6 "
7............	250	30	32	31	31.0	Grouped 1 hour
		33	32	33	32.6	" 2 hours
		25	25	25	25.0	" 3 "
		23	24	23	23.3	" 5 "
		18	20	20	19.3	" 6 "
8............	290	36	35	36	35.6	Grouped 1 hour
		33	33	30	32.0	" 2 hours
		30	31	30	30.3	" 3 "
		25	26	25	25.6	" 5 "
		23	21	25	23.0	" 6 "

low that of the aggregated snakes. This is well shown in a series of tests during which 5 *S. dekayi* were placed singly in the standard boxes lined with moist blotting paper. An aggregate of 5 snakes was placed in a similar box without the moist paper. The temperature was held constant and the respiratory rates recorded over a 9-hour period. As shown in Figure 7, the respiratory rate of the moist isolated snakes does not drop below that of the

aggregated. Hence the great drop in the respiratory rate of the isolated snakes on a dry substratum is to be attributed to water loss. More quantitative results concerning the significance of aggregation on respiration in *S. dekayi* have confirmed the above results (Clausen, 1934).

Effect of Humidity on Aggregation

Earlier in this series of studies it was noticed that when the gravel floor of the cages was wet, *S. dekayi* would not burrow. If the gravel was allowed to become very dry they would often be found entirely concealed in the gravel. It was apparent that humidity had an influence on the slow aggregation response which occurs in the absence of any disturbance factor. In order to secure more detailed information on the effect of humidity on this type of aggregation, we have tested a series of snakes in a tank equipped with an apparatus for controlling humidity.

An aquarium having the dimensions 36 x 40 x 60 cm. was provided with a close fitting glass top and sealed with stopcock grease. The aquarium had a bottom of Alberene stone and ends made of the same material. The sides and the top of the tank were of heavy glass. The glass top was held in place with tape. The tank was divided into 2 compartments of equal size by a glass partition which was raised 5 cm. from the gravel which covered the stone floor and thus allowed the snakes to move freely from one compartment to the other. A constant difference in humidity was maintained in the two compartments by pumping dry air into one and moist air into the other. Air was drawn out of each compartment from outlets at both ends of the aquarium by means of an electric pump. After bubbling this air through several vessels of water on one hand and passing it through one or two flasks of calcium chloride on the other, the air was returned to the two compartments of the tank.. The apertures for the air intake into the two compartments were made through the glass cover. Glass and rubber tubing carried the air into two large glass tubes which were 15 cm. in length and 4.5 cm. in diameter. One tube was laid on the gravel in the center of each chamber. These tubes will

TABLE 3. The aggregation response of *Storeria dekayi* in relation to humidity.

| Number of Snakes	Temperature in degrees C.	Per Cent Relative Humidity		Reaction	
		Wet Tube	Dry Tube	Wet Tube	Dry Tube
10.............	25	20	20	4	5
10.............	24	80	65	5	5
10.............	24	80	75	4	5
10.............	25	40	40	5	4
10.........`...`	24	40	20	6	4
12.............	24	35	25	5	5
14.............	25	67	43	1	9
10..............	24	40	32	4	6
10.............	24	70	28	0	8
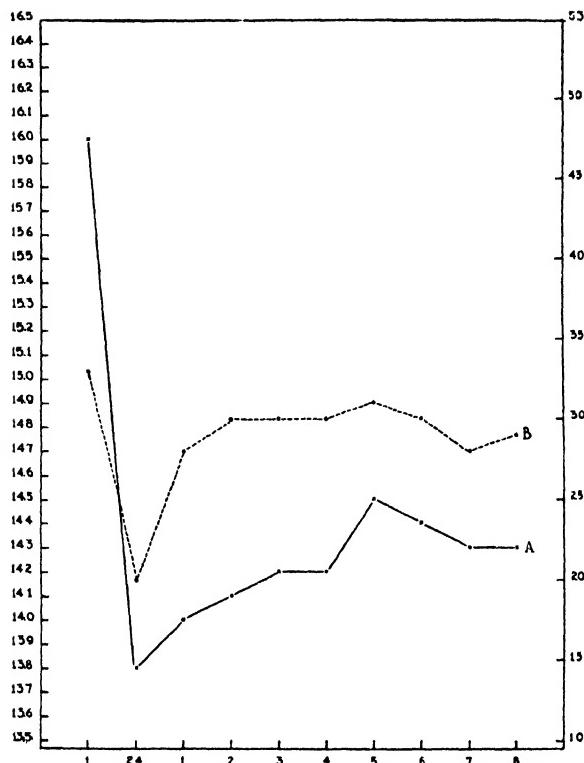
FIG. 6. Correlation between the respiratory rate and weight loss over a period of 32 hours at a temperature of 30° C. for aggregated *S. dekayi*. Abscissas, 1-24, hours in a dry container; 1-8 following, hours in moist container. Ordinates: left, weight in grams; right, respiratory rate. The continuous line A, weight; broken line B, respiratory rate.

be designated as either wet or dry tubes in the following records, depending on which receives the dry or moist air. A thermometer and hygrometer were placed in each compartment. These instruments were tested at frequent intervals throughout the experiment to make sure of their reliability.

In order to secure information on the sensory modalities employed in detecting moisture, a series of snakes with one or more sensory functions eliminated was also tested in this apparatus. In order to eliminate vision, the eyes, in some of the tests, were covered with adhesive tape which was usually blackened with India ink. In some tests a solution of 14 per cent collodion was darkened with ink and painted over the eyes. In a few tests a combination of both methods of blindfolding was utilized. The snakes frequently attempted to remove the blindfolds by rubbing, but after 24 hours they had usually given up these attempts. Tests were made only after 24

hours and only with snakes which showed no evidence of irritation from the blindfold.

The olfactory sense was eliminated by filling the nostrils with cotton plugs smeared with vaseline and then covered with collodion caps. In other tests the tongue, which has recently been shown to aid the functioning of Jacobson's organ, was severed just caudal to its bifurcation. These snakes were not utilized until they had apparently completely recovered from the operation.

In the following tables the results, as obtained with snakes having their sensory organs incapacitated, will be recorded as follows: B, blindfolded; N, nose-stopped; T, tongueless. Where more than one sense organ is eliminated, combinations of the above symbols will be used, i.e., BNT, blindfolded, nose-stopped and tongueless.

The reactions, as obtained under different humid conditions, for normal *S. dekayi* are recorded in Table 3. This table represents only the typical results obtained in a series of 21 tests. The number of snakes aggregating in or near the mouth of each tube is recorded in the table. If the snakes were in the mid-region of the tank no record was made of them. All individual records were made after the relative humidity had reached and maintained a designated point for 5 minutes. The results (Table 3) show that changes in moisture content of the chamber materially affect the aggregation response of snakes. It will be noted that in no case is the total number of snakes in each experiment accounted for at either the wet or dry tube. The reactions were recorded at the end of a 5-minute interval and if the time were extended the entire group would aggregate. When both tubes were of the same or nearly similar humid conditions the number of individuals around each tube was approximately the same irrespective of whether the humidity was extremely high or low. This condition is illustrated in the first 3 series of experiments in the table. When the relative humidity reached 20 per cent or lower the snakes showed a tendency to collect in the more moist region. They were usually active and irritable in this dry atmosphere and moved around continuously as though in search of a more moist region. When the relative humidity reached approximately 40 to 50 per cent the activity and irritation was again evidenced. In this case the snake seemed to be seeking a drier region. From the results of this series of tests, a part of which is illustrated in Table 3, it was concluded that in normal *S. dekayi* the typical grouping response occurs only when the relative humidity lies between 20 and 45 per cent.

For the series of *S. dekayi* with one or more of their sense organs eliminated, the experiments carried out exactly the same as in the normal series, showed that the same maximum and minimum humidity variations

produced similar results irrespective of the sense organs involved (Table 4). It may be concluded therefore, that the response to varying degrees of humidity was not in any way influenced by the sense organs which, as will be shown below, mediate the aggregation response.

TABLE 4. The effect of relative humidity on the aggregation of *Storeria dekayi* deprived of various sense organs.

*Series	Number of Snakes	Temperature in Centigrade	Percentage Rel. Humidity		Reaction	
			Wet Tube	Dry Tube	Wet Tube	Dry Tube
B........	10	25	75	40	2	5
	10	25	80	40	2	6
	8	24	45	35	4	4
	8	24	30	20	6	2
N........	10	24	80	48	2	6
	10	25	40	35	4	5
	10	24	30	20	4	1
T........	10	24	20	20	3	3
	10	24	35	21	6	1
	10	24	77	42	0	9
	10	25	76	68	4	4
BNT....	10	24	32	20	6	1
	10	24	79	45	1	9
	10	24	64	40	2	8
	10	24	45	38	5	5

*Type of experimental animal used:
    B - blindfolded.   N - nose-stopped.   T - tongueless.   BNT - blindfolded, nose-stopped and tongueless.

The same series of humidity experiments was carried out with *T. butleri*. The sensory functions were again eliminated in some cases and controls were employed as before. Again the eyes, nose, tongue or Jacobson's organs were found not to be indispensable. The range of adaptability to moisture, however, tended toward a higher percentage of relative humidity than in *S. dekayi*. In this species the response occurred between 30 per cent relative humidity as a minimum and 90 per cent as a maximum. These results therefore show that in respect to humidity, *T. butleri* not only have a higher range, but further, a more extensive range as compared to *S. dekayi*.

When snakes of either of the above species are first placed in the tanks and disturbed, the immediate tendency is toward a clustering irrespective of humidity. However, at almost the same time there is a change in the aggregate toward a more desirable region in respect to moisture. The tendency to aggregate on disturbance is apparently initiated and carried out without respect to moisture, but this response is only temporary and is dominated by a response to aggregate in regions of optimum conditions of humidity shortly thereafter.

TEMPERATURE AND AGGREGATION

In an early series of preliminary experiments it was noticed that by casting a strong light (400 watts) from a microscope lamp on the floor of a cage of *S. dekayi*, the snakes would not move into this area. The area illuminated in this case would have a temperature of 65° C. in the center. The above test was carried out at room temperature of 18 to 20° C. However, when the cage of *S. dekayi* was placed in a cooler room, 10° C., the animals would orient themselves around the illuminated area of the microscope lamp, the temperature of the illuminated area still being 65° C. The temperature of the illuminated area was then reduced to 20° C. by passing the light through a water chamber heat filter. When the temperature was reduced to 20° C. these snakes did not move toward the illuminated area. The light factor was then entirely eliminated and the temperature of the previously illuminated area increased to 60° C. In this case the snakes would again orient themselves around the heated area. It seems obvious from these tests that in *S. dekayi* light is not the primary factor but that the temperature also regulates the orientation.

The same experiment was repeated with *T. butleri*. When an area of the cage was illuminated at room temperatures of 18 to 20° C., these snakes would orient themselves around the illuminated area which again registered 65° C. at its center but graded into a wide area of lower temperature along the periphery. These snakes grouped nearer the hot center of the illuminated area than did *S. dekayi*. This was repeated under room temperatures of 10° C. and the same result as above was recorded. The heat factor was again eliminated as in the *S. dekayi* series and *T. butleri* oriented themselves in or as near as possible to the center of illumination. When the heat factor was introduced in the absence of light the orientation pattern was exactly the same as when both heat and light were employed.

From these experiments it is clear that *S. dekayi* will avoid a center of strong illumination while *T. butleri* will move across such areas. This difference in behavior is correlated with the habits of the two species, *S. dekayi* being the more nocturnal in habits.

It was found in the above experiments that temperature was of importance in directing the movement of both species of snakes. A series of tests was carried out to determine more fully the significance of temperature on the aggregation response. The same aquarium employed in the previous experiment on humidity was utilized again and the humidity was kept constant by the water vapor and calcium chloride apparatus described before. The temperature was controlled by means of an electric heater and all experiments were carried out in a dark room.

The snakes were placed in the aquarium and allowed to remain undisturbed for a period of 15 minutes at a constant humidity and temperature. At

the end of this period the number of individuals in an aggregation was tabulated on a percentage basis.   In all cases an aggregation consisted of a group of 3 or more of the total number of snakes.

The results presented in Table 5 show that the greatest percentage of aggregation takes place at temperatures ranging from 21 to 31° C.   Below 21° the snakes were sluggish and would remain in any one position for 5 or 6 hours and disturbance of any kind failed to induce reactions.   At temperatures above 31 and to 35° C. the snakes appeared irritable and uncomfortable.   They would crawl around the side of the cage continuously.   When disturbed at these high temperatures they would immediately react to stimulation by aggregation but the aggregates would break up as soon as left undisturbed and the snakes would continue to move about as before.   When the temperature rose above 35° C. the snakes were never found in aggregates or moving around.   They would usually be found extended along the edges of the cages.   Disturbance had no effect at these temperatures.

The above experiments were then repeated on *T. butleri* and similar results were obtained with the exception that aggregation reactions took place at higher temperatures.   The highest temperature at which aggregation occurred in this series was approximately 40° in contrast to 35° in *S. dekayi*.   The same difference is present at lower temperatures.   At 10 to 12° C., *T. butleri* reacted similarly to *S. dekayi* when the latter were subjected to a temperature of 7.2° C.   Below 10° C., *T. butleri* failed to aggregate when disturbed.

TABLE 5. The aggregation response in relation to temperature variations.

Number of Snakes	Trials	Percentage Rel. Humidity	Temperature Centigrade	Percentage Aggregation
10..............	3	40	7.2	50
10..............	4	40	10.0	50
10..............	5	40	10.0	40
10..............	5	40	12.0	50
10..............	6	40	15.0	40
20..............	5	40	17.0	30
20..............	6	40	19.0	55
20..............	5	41	21.0	75
10..............	8	40	23.0	80
20..............	6	41	25.0	80
20..............	5	40	27.0	95
20..............	5	40	29.0	70
10..............	8	40	31.0	70
10..............	6	40	33.0	40
20..............	5	40	35.0	20
20..............	5	40	37.0	..
20..............	6	40	39.0	..

In connection with the above temperature studies, the maximum temperature tolerance or temperature which would prove fatal to the snakes at a given humid condition was noted in both *S. dekayi* and *T. butleri.*   The

average maximum tolerance for 10 *S. dekayi* with the relative humidity at 35 per cent was 41° C. The variations in this group covered a range from 39 to 44° C. The average tolerance for *T. butleri* at 35 per cent relative humidity was 48° C. The variations for *T. butleri* were from 45 to 53° C.

From these studies it may be concluded that aggregation takes place normally within a more or less definite temperature range and that the response to disturbance is more stimulating at certain definite temperatures. Here again, when disturbance factors are introduced they dominate over temperature responses but the response at unfavorable temperatures is very temporary. *T. butleri* forms typical aggregations at higher temperatures than the optimum for *S. dekayi*. Furthermore, the temperature tolerance of the first species is approximately 7° C. higher than that of the second.

THE RÔLE OF THE SENSE ORGANS IN AGGREGATION

Since the aggregation response is quickly evoked in *S. dekayi* even when the snakes are widely scattered about the cage, it is apparent that some distance receptor must play a part in the reaction. In order to determine which receptor or combination of receptors is directly involved in the response, the functioning of the various sense organs was eliminated, as in the humidity experiments, either singly or in combination, and the effect upon the aggregation response recorded.

Vision, olfaction and the tongue were eliminated as previously described. Jacobson's organ was destroyed by cauterization following etherization. The operation was checked by a study of serial sections of the heads of the snakes treated, and the Jacobson's organ was found to be completely destroyed in these cases. The mortality from this operation was less than 10 per cent. No cauterized snakes were used in the tests until two weeks after operation when they were feeding normally.

The snakes to be tested were placed in glass-sided cages measuring 12 x 21 x 14 cm. A layer of slightly dampened gravel was spread over the floor of the cage. Some of the cages were maintained in a photographer's dark room and others in a well lighted room. Aggregation was induced in some cases by either suddenly shaking the cage or merely tapping one of the glass sides. This was continued for a period of 3 minutes and the distribution of the snakes recorded. Since under these conditions there was always a certain amount of shifting and reforming of the aggregations it was only rarely in the controls that all the snakes were found to be aggregated at the termination of the 3-minute period. On the other hand when the snakes were moving at random about the cage a few at any one moment might be temporarily in contact. Hence we have taken an arbitrary standard of 90 per cent of the total number of snakes aggregated as a positive reaction and of less than 20 per cent as negative reaction. In our first series of tests tab-
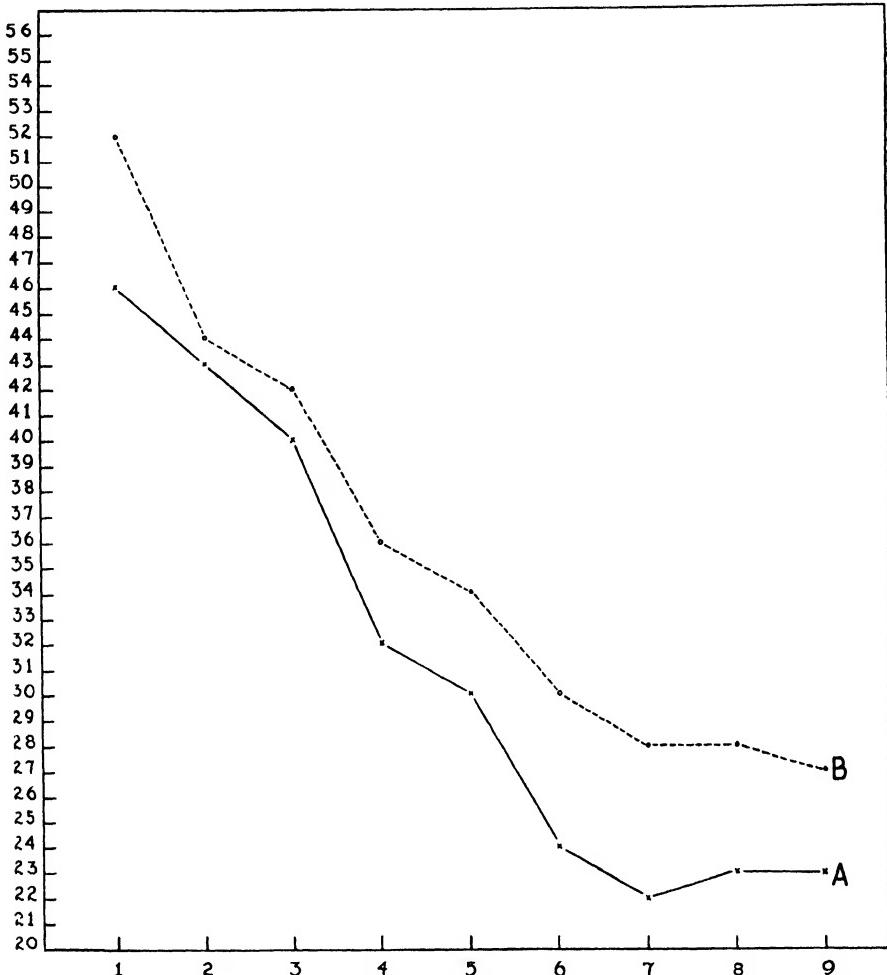
FIG. 7. The average rate of respiration of five *S. dekayi* in an aggregated condition in a container at 30° C. over a 9-hour period in comparison to 5 isolated *S. dekayi* in containers at the same temperature for a similar period, the aggregate being kept dry and the isolated moist. Broken line B, the isolated; continuous line A, the aggregate; abscissas, hourly period; ordinates, respiratory counts per minute.

ulated below, the room temperature was approximately 21° C. The relative humidity was maintained at 45 per cent throughout the entire period of this set of experiments. In Table 6 the same series of abbreviations are employed as have been used in Table 4. These will be employed throughout this paper to indicate snakes with one or more sensory functions eliminated. In each series, under both light and dark conditions, aggregation was induced with the experimental snakes in the same cage with control snakes. The controls were then removed and the same test repeated. In no case, as recorded in Table 6, were the reactions of the experimental snakes affected by the presence of the controls.

From Table 6 it is clear that in the blindfolded series all trials gave definite aggregations. No difference was noted between the light and the dark room series as regards the average time taken for aggregation. It was, however, quite evident that the reaction time was much slower in the cases of this experimental series than for the controls. It required nearly 3 minutes for the experimentals to aggregate while the controls with their unobstructed vision reacted almost instantly. In the nose-stopped series very different results were obtained. The tests made in the dark room gave no aggregation response in contrast to those made in the light room. The two groups were left in the dark room over night, and the following morning 10 of the 14 controls and 4 of the 10 experimentals were found in two clusters

TABLE 6. The influence of sense organs on aggregation.

*Series	**Room	Number of Snakes		Trials	Reaction
		Experimental[1]	Control[2]		
B	L	15	0	3	Positive
B	L	15	10	3	Positive
B	D	15	0	4	Positive
B	D	15	10	3	Positive
N	L	14	0	3	Positive
N	L	14	10	3	Positive
N	D	14	0	8	Negative
N	D	14	10	3	Negative
T	L	12	0	4	Positive
T	L	12	10	5	Positive
T	D	12	0	4	Positive
T	D	12	10	4	Positive
BN	L	14	0	5	Negative
BN	L	14	10	5	Negative
BN	D	14	0	4	Negative
BN	D	14	10	4	Negative
BT	L	12	0	4	Positive
BT	L	12	10	3	Positive
BT	D	12	0	2	Positive
BT	D	12	10	3	Positive
NT	L	11	0	3	Positive
NT	L	11	10	5	Positive
NT	D	11	0	5	(4) Negative
NT	D	11	10	5	Negative
BNT..........	L	11	0	4	Negative
BNT..........	L	11	10	4	Negative
BNT..........	D	11	0	3	Negative
BNT..........	D	11	10	4	Negative

*Designates type of experimental animal used, i.e., - B, blindfolded; N, nose-stopped; T, tongueless; BN, blindfolded and nose-stopped; BT, blindfolded and tongueless; NT, nose-stopped and tongueless; BNT, blindfolded, nose-stopped and tongueless.
**L - Daylight (in front of window); D - Darkroom.
[1]Animals from which sensory structures were removed.
[2]Untreated animals.

while the remaining 6 experimentals were scattered over the entire cage. Hence it was clear that plugging the nostrils had a very definite effect of delaying, if not preventing, the aggregation response.

In the tongueless series the tongues had been removed from the 12 individuals 5 days before the experimental data were recorded. In this series 17 tests were positive and the snakes all aggregated into 1 or 2 groups. However, the reaction time as recorded tended to be somewhat slower under the dark conditions. In view of the reported importance of the tongue in the sensory life of snakes it was of interest to find that removing the tongue did not prevent the snakes from aggregating in the dark.

In the blindfolded and nose-stopped series all reactions were negative. Of the 18 tests made under both light and dark conditions, as well as in supplementary tests where the snakes were left over night in the dark room, no signs of aggregation were noted. This was also true even though the snakes frequently came in contact with one another while wandering about the cage. They would crawl over one another in the same indifferent way as when coming in contact with sticks or pieces of wood placed in the cage. In this group of blindfolded and nose-stopped snakes the tongue was protruded more rapidly and more extensively than in the controls.

In the nose-plugged and tongueless series the results were very different whether or not the cages were placed in the dark room or in the light. All the daylight tests gave definite aggregation responses while 90 per cent of the dark room tests were negative. The one positive result in the series of 10 trials of the dark room series requires further comment. At the end of the 3-minute stimulation period there were 6 snakes in one cluster, 8 in another and one isolated. These same individuals were left over night in the same cage with 10 controls. In the morning all the controls had aggregated but only 30 per cent of the nose-plugged and tongueless individuals were grouped.

We may conclude from the data listed in the above table that vision and, less extensively, olfaction, are the chief senses which enter into the aggregation response. The tongue plays little or no part in the response. Since the tongue is believed to have important functions in the food seeking reactions of other snakes we may return to the question of the function of the tongue in *Storeria* after we have examined its feeding behavior. So far as aggregation is concerned vision is the chief aid to a rapid response. The question remains nevertheless as to how specific the visual cues must be to evoke an aggregation response.

EXPERIMENTS WITH MODELS AND NARCOTIZED INDIVIDUALS

In order to test whether or not the aggregating snakes were reacting to some external feature which helped to make up the general appearance of the species a series of tests was made with narcotized individuals with whole
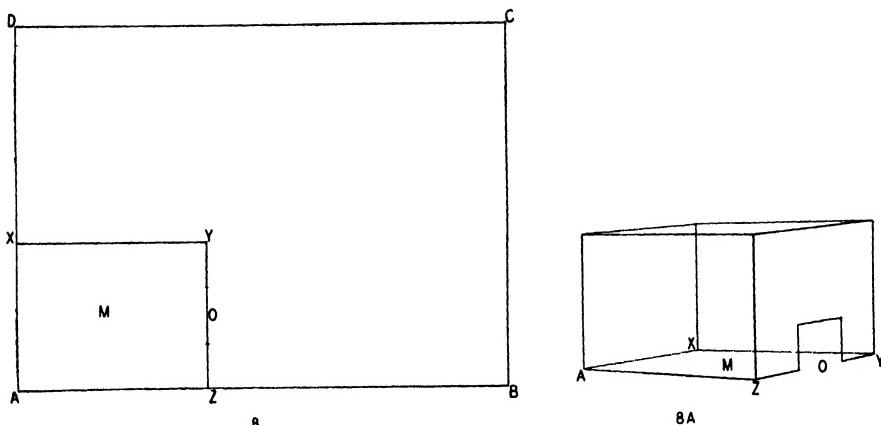
FIG. 8. Diagram showing how the glass plates XY and YZ were arranged at right angles in cage ABCD. M, the region where the aggregate was placed. O, the aperture used in some of the experiments as outlined. 8A, a side view.

specimens infiltrated with paraffin, and with colored wax casts. The casts and the infiltrated specimens were taken from the exhibition hall of the American Museum and represented a very close approximation to the living *S. dekayi*. The narcotized snakes were injected with a 5 per cent solution of cocaine.

Eight normal and 8 other snakes having one or more sensory organs incapacitated were placed in the cages with 5 narcotized snakes or with 5 infiltrated specimens or casts. A reaction was interpreted as positive when at least 5 of the 8 normal or 5 of the 8 experimental snakes remained in contact with the models or narcotized forms for a period of 5 minutes. This was a different criterion of aggregation from that utilized in the previous tests but in view of the fact that the models and narcotized individuals were held motionless during the test the conditions of the experiment were different from those reported above and hence a new criterion of aggregation seemed desirable.

In one series of tests the snakes with functional sense organs were immersed in a 10 per cent solution of magnesium sulphate for the purpose of anaesthetizing the skin. The treatment was repeated with a series having the nostrils plugged, the tongue removed and the eyes blindfolded. It was previously found that this treatment rendered normal snakes more sluggish in all their movements but did not prevent aggregation. It seemed to follow, that in snakes equipped with the eyes, nose and tongue, skin sensibility did not enter into the aggregation response. It nevertheless seemed possible that the tactile organs of the skin might enter into the discrimination of active from quiescent snakes and hence the treatment was repeated on some of the individuals employed in the following experiments. In Table 7 the same ab-

breviations are utilized as above. In addition "U" refers to the untreated individuals having all their sense organs intact and "A" to the series with anaesthetized skin.

The tests as tabulated above demonstrate that *Storeria* will not aggregate with quiescent individuals of the same species whether these be narcotized individuals or infiltrated specimens or models. Whether this is due to a lack of reciprocal movement on contact or to the lack of bodily movement before contact is not brought out by these particular tests. Tongueless *Storeria* reacted exactly like the intact controls. Over the entire series of tests where the nostrils were closed the results were quite diverse. In 66 per cent of these cases the experimentals aggregated with the models and the narcotized individuals. Forty-two per cent of this series reacted positively under dark room conditions. This indicates that vision plays some part in the process of differentiation between live forms and models or narcotized forms. Since there was only a 3 per cent difference in the response to the narcotized indi-

TABLE 7. Aggregation with models and narcotized forms.

Series	Trials	With Models				With Narcotized Forms			
		Daylight		Darkroom		Daylight		Darkroom	
		+	—	+	—	+	—	+	—
U	10		—		—		—		—
B	10		—		—		—		--
T	10		—		--		--		—
BN	16	3	1	4		2	2	4	
N	16		--	2	2		—	2	2
NT	16		4	3	1	1	3	3	1
BNT	20	4	1	3	2	3	2	5	
BT	10		—		—		—		—
A[1]	15		—		—		—		—
BNT[1]..........	18	2	3	2	2	4	2	1	2

[1]Abbreviations as in Table 6 In addition to these—
    U, Untreated. A, Skin anaesthetized with 10 per cent magnesium sulphate.

viduals compared to that of the models it would appear that when the nostrils are closed *Storeria* is unable to discriminate between them in the dark.

EXPERIMENTS WITH GLASS PLATES AND MIRRORS

In the aggregation response of *Storeria* vision appears to play a dominant rôle but as shown above the snakes will not aggregate with narcotized individuals or with models. They also do not respond to freshly killed individuals. Hence it is apparently the movement of some of the snakes in any one group which calls forth the aggregation response. In order to test this conclusion we devised another series of experiments.

In the first experiments a group of intact *Storeria* was separated from others in the cage by means of a glass plate partition. Figure 8 shows how

the glass was placed in the cage. Two glass plates, XY and YZ, were arranged at right angles in one corner of the cage. A cluster of snakes was then placed in the region M. A similar number of snakes was distributed in the area YC. The snakes in region YC were then disturbed and all but a very few of them invariably moved to the aggregation already formed in region M enclosed by the glass plates. This test was repeated 10 times and an average of 80 per cent of the total number of snakes in region YC moved toward the aggregate M. These moving snakes made deliberate efforts to pass through the glass plates toward the aggregation. They would run into the glass and then move along the sides of the plate and in some cases attempted to crawl up over the plates.

All the snakes in both region M and YC were then blindfolded. The individuals in region M were allowed to aggregate first and the snakes in area YC were disturbed as previously. Instead of moving toward the already formed cluster in region M, they aggregated within their own group in region YC. No attempts were made to pass through the glass plates to region M. When these snakes were only nose-stopped, reactions were exactly the same as in the normal series in the daylight. However, nose-plugged snakes, when placed in a dark room failed to move towards the glass partition and only about 40 per cent of each group aggregated within their own region.

In the next series of this group of experiments a square 5 x 5 cm. was left clear in the glass plate XY, and the remainder of the glass plate XY, as well as all of YZ, was covered with black paper.

Figure 8A shows a side view of the right angle partition indicated in Figure 8. In this experiment the snakes were again placed in M and YC. When the normal snakes in YC were disturbed they tended to aggregate into one cluster unless one of the group happened to see the cluster in M through the clear glass O. In this case the individual would move in the direction of O. In 6 out of 12 trials the snakes in area YC aggregated in front of O, the clear portions of the glass XY. In no case did the animals attempt to crawl up the darkened portion of the glass plates but frequently ran against the clear area O.

In the next series of experiments, instead of employing a glass partition, a cardboard of the same size as XY was substituted. In this partition an opening of the same size as aperature O was cut. The cardboard was colored black, and the snakes utilized in the preceding experiment were tested in this apparatus. In these tests the normal snakes all passed through the opening O without attempting to form an aggregate outside of the aperture. The tests were then repeated on blindfolded animals with the result that they all passed through the opening in the same manner as the normals but more slowly. When a series of nose-stopped individuals was substituted for the blindfolded and the tests repeated in the daylight, the movements were exactly
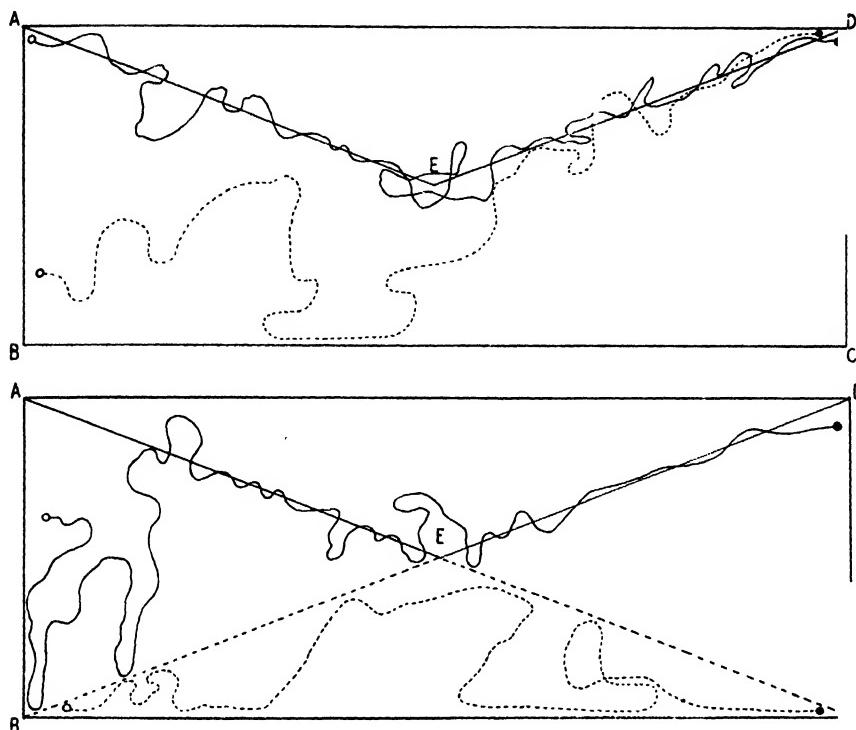
FIGS. 9 and 10. Figure 9 shows the trails of two male *S. dekayi* starting at AB and ending at D. Trail AED was made by rubbing body integument over the course. Figure 10 shows the same two male snakes beginning at AB. AED scented with body integument. Trail BEC scented with cloacal gland secretion.

the same as for the normals in the daylight. When the apparatus was shifted into the dark room no snakes passed through aperture O. The entire series responded similarly to the blindfolded, nose-stopped individuals.

Although the above experiments clearly indicated the importance of vision and the secondary rôle of olfaction in the aggregation response these conclusions were tested further by means of mirrors. When a *Storeria* with all the sense organs intact was placed in a cage containing a mirror it would almost invariably come to rest in front of the mirror. If the position of the mirror was changed and the snake disturbed it would move with some rapidity to the side of the mirror and would remain there for several hours if left undisturbed. It would seem from this experiment that the attraction of a mirror for a disturbed snake was almost as great as the presence of another snake. Further tests, however, disclosed a difference, for when groups of *Storeria* were placed in the cage containing the mirror, the snakes did not always aggregate in front of the mirror. Out of 15 such trials, 8 cases of 100 per cent aggregation occurred in front of the mirror. In the other 7

trials 1 or 2 of the snakes were found in front of the mirror while the main cluster was gathered in another region of the cage.

Two mirrors were then placed at right angles to one another in one corner of the cage. One snake was then placed in the cage and disturbed. The snake would invariably move up in front of one of the mirrors. Two snakes were then placed in the cage, one of them being placed in front of each of the mirrors. When disturbed they would always aggregate in one cluster regardless of the images in the mirror. It follows from these experiments that an active *Storeria* is a greater attraction to another than the mirror image of either one.

When this test was repeated with a normal *Storeria* and an infiltrated model the normal snake reacted indifferently to the model in 75 per cent of the cases but would make contact with the mirror. In the other 25 per cent of the cases it aggregated with the model. The model was then removed and a stick of wood or a piece of rubber tubing substituted. The results were the same as for the model.

When the infiltrated specimen was removed and a group of blindfolded *Storeria* was placed in front of the double mirror the snakes again aggregated among themselves as in the case of the normals and not with the mirror images. All of the above experiments with the right angle mirror were carried out in the daylight. When this series of tests was repeated in the dark room no aggregation against the mirror occurred in any case.

It seemed possible that a *Storeria* might prefer an active snake to its own image merely because the active snake was moving differently from itself. We have tested this question by another series of tests. A mirror was fastened at either end of the cage and a group of normal *Storeria* was placed in the mid-region and disturbed. In over 20 such tests the results gave no evidence of a difference as regards regional preference. That is, approximately 50 per cent aggregated at either end or the majority would aggregate at one or the other ends of the cage approximately the same number of times. Then glass plates were substituted for the mirrors and a single snake placed behind each one. When a pair of snakes was placed before the glass plates which were held at right angles to one another, the two snakes would move together to make contact and did not attempt to aggregate with the snakes behind the glass. Hence a snake behind a glass plate is no more attractive to another than is the mirror image of the latter. We ruled out any effect which the texture of the glass might have on the *Storeria* by performing a supplementary series of experiments in which the mirror was placed behind a glass plate. This did not modify the results in any way.

The above experiments with mirrors and glass plates clearly indicate that while vision is of great importance in aggregation the response is more vigorous when aided by some other factor. The experiment with the nose-stopped

series indicates that this secondary factor is olfaction. Since normal *Storeria* attempt to aggregate with other active individuals behind glass we have further evidence of the primary importance of vision in the response.

THE RÔLE OF COLOR IN AGGREGATION

Most species of snakes are distinguished by a particular color pattern which is not found in any other forms. The four species utilized in this study are readily identifiable by color pattern alone. There is frequent reference in the natural history literature to the color pattern of vertebrates as aiding species in identifying their own kind. Since vision plays the most important rôle of color in the aggregation response of *Storeria* it seemed desirable to test the rôle of color in species identification.

A series of *Storeria dekayi* and *Thamnophis sauritus* was selected and 3 individuals of both species were dyed green by using a dilute solution of mercurochrome. The same number of each species was stained blue by using 1 to 10 per cent solutions of methylene blue. The same number was stained red by painting with a 1 per cent aqueous solution of eosin, and yellow by using a saturated solution of chrome yellow. None of the above stains seemed to irritate the snakes which reacted in the normal manner when the dye was dry. These stains did not entirely remove the original color pattern but in all cases the stain, when applied uniformly over the entire body, would change the pattern by obscuring certain elements.

A group of 3 to 5 *S. dekayi* was placed in a cage with a group of painted snakes. The snakes were then disturbed as in the previous experiments and the number of snakes aggregating after a 3-minute interval was recorded. It will be noticed in the following table that *S. dekayi* when provided with its complete sensory equipment will aggregate as readily with individuals of its own species colored bright yellow, blue, red or green as it did previously with uncolored individuals. On the other hand, *S. dekayi* will not aggregate with *T. sauritus* when the latter is stained with the same dyes. The 10 per cent amount of contact recorded in Table 8 falls within the limits of chance contact in any group of non-aggregating snakes. It will be noticed from the table that plugging the nostrils (N series) greatly lowers the amount of aggregation within the *Storeria* snakes during the 3 minute period. Further, the same operation increases the amount of aggregation between *S. dekayi* and *T. sauritus* during the same period.

The above color pattern experiments therefore show that while vision plays an important part in aggregation, the olfaction is also to be considered as an important sensory factor in this behavior. It can also be noted above that color pattern identification in respect to species recognition is not of primary importance but that olfaction is again a dominating sense in this respect.

Table 8. Color pattern variations and aggregation.

Species	Colored Snakes		Test Snakes *S. dekayi*		Trials	Percentage Aggregation
	Number	Color	Number	Kind		
S. dekayi	3	Yellow	3	U	4	100
S. dekayi	3	Blue	3	U	4	100
S. dekayi	3	Red	3	U	3	85
S. dekayi	3	Green	3	U	3	90
S. dekayi	3	Yellow	3	B	4	90
S. dekayi	3	Red	3	B	3	100
S. dekayi	3	Blue	3	B	3	90
S. dekayi	3	Yellow	3	N	3	50
S. dekayi	3	Blue	4	N	4	40
S. dekayi	3	Red	4	N	3	35
T. sauritus	3	Yellow	4	N	5	20
T. sauritus	3	Green	4	N	4	30
T. sauritus	3	Yellow	3	U	5	10
T. sauritus	3	Yellow	4	B	4	10
T. sauritus	3	Yellow	4	NT	4	25
T. sauritus	3	Red	5	NT	3	20

Species Identification in Aggregation

If a series of *S. dekayi* and of *T. sauritus* are placed together in a cage the two species will separate out and each will form one or more aggregations distinct from those of the other species. If an individual of either species is gently placed within the aggregation of the other species it will not remain there but will soon seek its own kind. When the aggregations are left undisturbed for long periods, individual snakes which have freed themselves from the clusters may be seen to make contact with the aggregations of the other species but they rarely, if ever, settle down to remain in contact with these foreign aggregations. In brief, there is a well-marked species factor in the aggregation response.

The previous experiments with colored snakes indicated that olfaction functioned to a large extent in species identification. In order to test this function further a series of *S. dekayi* and another of *T. sauritus* were blindfolded, other series had the nostrils plugged or the tongue excised as in previous experiments. Then a group of snakes including both species was mixed and placed together in a cage. After a 3-minute period of disturbance the amount of aggregation within each species and between the species was recorded. The results are tabulated in the following columns (Table 9).

The table shows that when the two species are only blindfolded or only nose-stopped there is no great decrease in the percentage of aggregation during the 3-minute period. An elimination of both olfaction and vision enormously decreases the percentages of aggregation within the species. This is merely confirmation of results obtained in previous tests. Of special interest was the fact that in all cases where the nostrils were plugged in both species
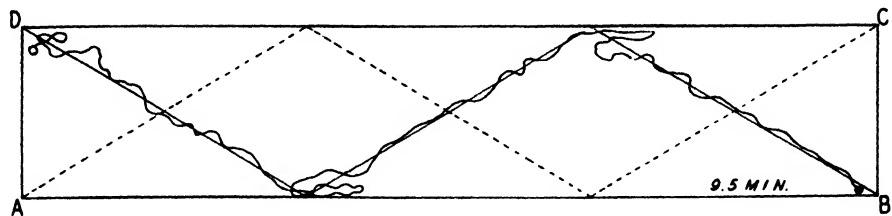
Fig. 11. Trail of normal *S. dekayi* beginning at D and ending at B with the time required to cover the trail.
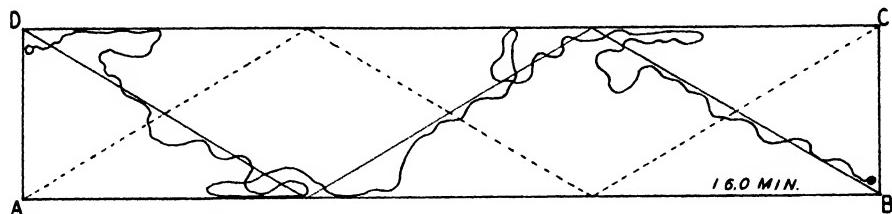

Fig. 12. The trail of an untreated *T. sirtalis*.
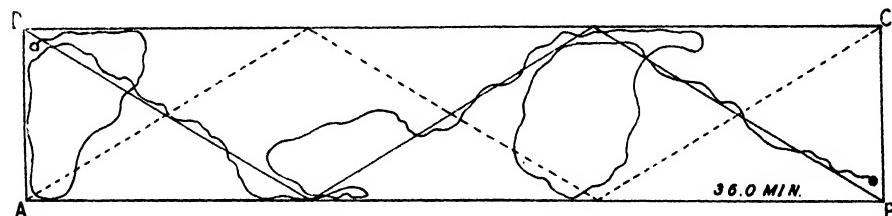
Fig. 13. The trail of an *S. dekayi* with olfaction eliminated.
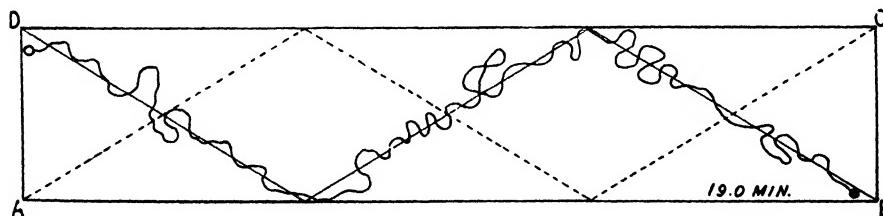
Fig. 14. The trail of an *S. dekayi* with Jacobson's organs incapacitated.
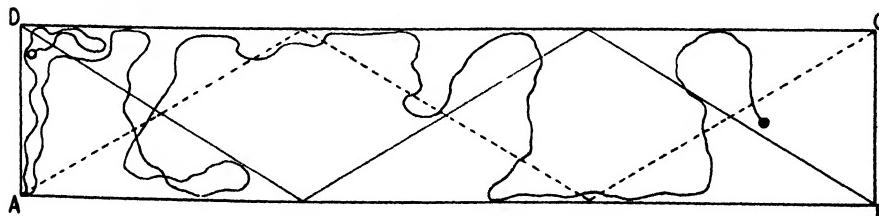
Fig. 15. The trail of an *S. dekayi* with both Jacobson's organs and the olfactory organs incapacitated. No time reaction is listed here since the trail was not followed from D to B and the time involved here was not significant.

Figs. 11-15. Diagrams of soapstone surfaces. Continuous line in the area, the food scented trail; broken line, the distilled water trail.

TABLE 9. Inter-species identification experiments.

S. dekayi	T. sauritus	Number of Snakes in Series		Number of Trials	Percentage Aggregation		
Series A	Series B	A	B		A	B	AB
U	U	10	6	5	80	100	0
U	B	10	6	4	90	100	0
B	U	10	6	3	80	80	0
B	B	10	6	4	70	80	0
B	N	10	6	4	80	65	0
NT	U	5	4	7	72	82	0
NT	NT	5	3	8	68	85	25
N	N	8	6	4	60	72	35
BN	BN	8	6	4	45	55	50
BNT	BNT	8	6	5	35	45	40
T	T	6	5	4	90	90	·0

a certain percentage of aggregation between the species occurred. When the tongue alone was removed no aggregation between the species took place. This would indicate that the tongue plays no part in species identification.

THE SIZE FACTOR IN AGGREGATION

It has been shown in the preceding experiments that a snake will not aggregate with another species if its olfactory functions are unimpaired. Conversely, when the nostrils of two species were plugged, the percentage of aggregation greatly increased. In nature snakes frequently show very little of their bodies when crawling through the grass or other cover. This, therefore, raises the question of whether a small portion of the body of another species would serve as a source of attraction if odor was excluded. Before attempting to answer this question it seemed important to establish the amount of a snake's body which would attract individuals of its own species.

To establish this point a glass tube 15 cm. in length and 4 cm. in width was sealed at one end and fitted with a tight rubber stopper at the other. After inserting a DeKay's snake within the tube the outside of the tube was wrapped with a strip of black paper 1 cm. in width. The paper was wrapped in such a way that it could be slipped back and forth on the tube, exposing various portions of the enclosed snake. The tube was then suspended about 1 cm. above the gravel floor at one end of the cage and a similar tube containing no snake was suspended in a like manner at the other end of the cage. Another DeKay's snake was placed in the cage midway between the two tubes and the movements of this snake recorded with respect to the enclosed snake and the control tube. The position of the glass tubes was frequently changed but data recorded in Table 10 were taken for only a single position because the length of time required to make contact with the tube naturally varied with the distance of the snake from the tube.

It will be noted in the following table that a *Storeria* will come in contact with the glass tube when only 40 mm. of the enclosed snake's body is exposed. When this area is reduced to 10 mm. in length no aggregation response will occur. At least in 5 trials the free snake never came to rest in contact with the glass tube having 10 mm. of the enclosed snake's body exposed to view. A blindfolded *Storeria* will not respond even though all of the enclosed snake's body is exposed. When the *Storeria* within the glass was stained yellow or blue the free snake with unobstructed vision made contact with the tube in the average time of one minute even though only 150 mm. of the tube snake was visible.

When a *T. sauritus* or a *T. sirtalis* was placed in the tube and sealed the same aggregation response was induced in the free *Storeria* as when another *Storeria* was within the tube, but the time required for the response was greater. In other words in the absence of odor *Storeria* will attempt to aggregate with a foreign species but more slowly than it would with its own kind in the tube. It is possible that this time difference is due to the fact that all adult *Storeria* have reacted so frequently toward their own species that they are, to a certain extent, conditioned. However, our experiments have not been sufficiently numerous to determine what influence, if any, learning has on the aggregation response.

TABLE 10. The visual response in respect to the size of the object.

Tube Snake		Exper. Snakes		Mm. of Tube Exposed	Trials	Reaction	Reaction Time (sec.)
Species	Size mm.	Number	Condition				
S. dekayi	150	1	U	150	3	Positive	45
S. dekayi	150	1	U	75	2	Positive	110
S. dekayi	150	1	U	40	4	Positive	120
S. dekayi	150	1	U	10	5	Negative	...
S. dekayi	150	1	B	150	3	Negative	...
S. dekayi	150	1	B	15	2	Negative	...
S. dekayi*	150	4	U	150	3	1 Positive	240
S. dekayi	150	4	U	75	3	Positive	300
S. dekayi	300	1	U	150	3	Positive	40
S. dekayi	300	1	U	75	2	Positive	60
S. dekayi	300	4	U	150	3	Positive	180
S. dekayi	300	4	B	150	4	2 Negative	...
S. dekayi**	200	1	U	150	3	Positive	60
S. dekayi***	200	1	U	150	3	Positive	60
T. sauritus	300	1	U	150	3	Positive	60
T. sauritus	300	1	U	75	3	Positive	115
T. sauritus	300	4	U	100	3	Negative	...
T. sirtalis	270	1	U	150	5	Positive	90
T. sirtalis	270	4	U	150	4	Negative	...

*One snake went to tube snake in 3 trials. **Tube snake colored yellow. ***Tube snake colored blue.

It will also be noted from the above table that when several snakes are placed in the cage together at some distance from the tube they will attempt to aggregate among themselves and not with the snake in the tube. This

seems to indicate that when odor is present to facilitate any impulses derived from optic stimulation, the response is towards the source of this double stimulation.

The experiments summarized in the above table show that while the visual impression serves as a source of attraction during aggregation the species identification is accomplished primarily by some other receptor mechanism. Since *Thamnophis* will attract *Storeria* when sealed in a glass tube it would seem highly probable that species identification is accomplished primarily by odor.

The Relation of Aggregation to Efforts at Concealment

As stated in the earlier paragraphs of this report the aggregation response of the extreme type employed to some extent in this study is far less commonly seen in nature than a less vigorous response which leads one individual to seek others of its kind when these are hidden. *S. dekayi* will readily bury itself in the dry gravel on the floor of the cage but in doing so it will usually seek the same part of the cage already occupied by others of its species. If a group of snakes were already concealed, vision would not enter at all into the response. Such behavior appears at first more like an attempt to reach suitable cover than to aggregate. It seemed desirable to treat the sense organs entering into this response with a view to throwing further light on the nature of the reaction.

Early in our experiments it was found that *Storeria,* when placed in a glass-sided cage employed in this study, would endeavor to hide beneath a cross piece of wood which held down the gravel filled tray of the cage. When several snakes were placed together in the cage they would frequently soon begin to disappear under the gravel at this end of the cage. This attempt at concealment was observed several times and in no series of cases did a particular individual assume leadership in the "march" toward the cross piece. The snake nearest the bar usually took the lead and was then followed by the remainder of the group. When the frame was completely covered with gravel the snakes would burrow through it in an effort to hide. When a hole was made in the gravel under the cross piece, this aperture was always selected by the first snake to reach it and the other snakes followed the leader down the hole, the group spreading out under the cross piece. The time required for the first snake to enter and completely conceal itself was approximately twice that taken for the second to complete the same process when both were the same distance from the bar. Records were kept of the time required for the complete concealment of 10 individuals over a series of 6 trials. The average time was 4 minutes at a temperature of 24° C. However, at a lower temperature of 13° C. the average time required was 6.2 minutes over a series of 7 trials. The same experiments were carried out in the dark room and in a

series of 5 trials the average time for complete concealment was 9.1 minutes at 24° C.

A series of *S. dekayi* having the eyes blindfolded, the nostrils plugged or the tongues excised was used and the time required to enter the hole under the cross piece recorded. The experiment was run at 28° C. under both dark and light conditions. Table 11 records the results of the above experiment. These experiments show that vision is the primary functional sense organ used by one *Storeria* when placed in a cage and required to find the aperture leading under the cross piece under which another *Storeria* has previously been placed. However, olfaction also is functional since there is a difference in time required for concealment of the nose-stopped snake as compared with the untreated. When vision and olfaction are both eliminated as in the case of the nose-stopped series under dark conditions the snake in all cases failed to enter the aperture.

TABLE 11. Speed of concealment in relation to the sense organs involved.

Series	Room	Individual Trials (Time in min.)						Average Time*
U	Light	3.5	3.0	3.0	4.5	5.0	5.5	4.0
B	Light	10.0	12.0	10.5	11.0	12.0	...	11.1
N	Light	7.0	5.5	5.0	6.5	....	...	6.0
N	Dark	0.0	0.0	0.0	0.0	0.0	0.0	0.0
T	Light	4.0	4.5	4.5	5.0	3.5	...	4.2
T	Dark	12.0	9.5	11.5	10.0	10.0	...	10.2
BNT	Light	0.0	0.0	0.0	0.0	....	...	0.0

*All tests carried out at room temperature, 24° C.

At the conclusion of this series of tests the gravel on the floor of the cage was thoroughly moistened with water. The tests were then repeated in both the light and dark. Only about 30 per cent of the *Storeria* which had entered the hole under the cross piece previously would repeat this response when the gravel was thoroughly moistened. Moreover, the time required was 3 to 4 times longer. Turning the cages at various angles to the light did not affect the results.

The degree of moisture has, therefore, a marked influence on the efforts of *Storeria* toward concealment by burrowing. By introducing blocks of wood of various sizes in the cages it was found that the size of the block also has an influence since fewer snakes will cluster under the smaller than under the larger blocks. The presence of a hole leading under the block is not an essential requirement. Once a snake is concealed below a block of wood placed anywhere in the cage this block becomes more attractive than any other similar block in the same cage. The question was raised as to whether olfaction or some other sense was employed to find these completely hidden snakes. To answer this question a new series of tests was devised.

A series of *S. dekayi* was placed in cages containing very dry gravel but no moss. The temperature was 26° C. and relative humidity 20 per cent. Under these conditions the snakes would always seek cover. The end cross piece of the cage in the absence of other blocks, offered a means of retreat. One snake was placed in the cage and it would move to this end of the cage and burrow through the gravel to work its way under the cross piece. When this snake had completely concealed itself, the hole it had made in the gravel was smoothed over and another snake placed in the cage and its movements observed. This snake would move in the same direction, and in 90 per cent of the cases would burrow through the gravel in the same region as the first. This was repeated for 3 more snakes with the same result. The experiment was then repeated with snakes having one or more sense organs incapacitated. We have included in these tests, snakes with Jacobson's organs destroyed by cauterization. The data recorded in the last column of Table 12 give the average time required for the third snake of the series of 5 snakes in each series of trials to burrow out of sight near the two snakes which had been released previously one after the other.

TABLE 12. Concealment following the elimination of particular sense organs.

Series*	Trials	Reaction	Percentage	Time in Seconds
U	8	Positive	90	150
T	5	Positive	80	175
B	7	Positive	85	240
BT	7	Positive	72	310
BN	9	Positive	12	720
NT	8	Positive	20	520
BNT	12	Positive	16	630
N	9	Positive	12	600
BNJ	10	Positive	10	830
BNJT	10	Negative	..	...
BJ	10	Positive	80	205
NJ	10	Positive	10	900 plus

*Usual series abbreviations with the addition of J, which designates the removal of Jacobson's organs.

This series of experiments shows that in any series of tests where the olfactory sense is incapacitated the reaction is either entirely or partially disrupted. The trailing is accomplished chiefly by olfaction, with the tongue and Jacobson's organ functioning as secondary recipient structures.

The Nature of the Olfactory Stimulus to Aggregation

Although it has been shown in the preceding experiments that olfaction plays a part in aggregation and is the chief sensory mechanism for discriminating between species, no attempt was made above to localize the source of the odor to a particular part of a snake's body. It is well known that snakes are provided in both sexes with cloacal glands which produce a highly odorous substance having frequently a distinctive color and usually a de-

tectable difference in odor in the different species. It is no wonder that many naturalists such as Prater (1933) have suggested that one of the functions of these glands is to help a species in finding its own kind. However, we have never seen even the blindfolded snakes, when aggregating, seek the cloacal region of another snake in preference to some other part of the snake's body. Hence it seemed desirable to determine by experiment if one part of a snake's body is more attractive than some other part to an aggregating snake.

When a blindfolded *Storeria* was placed in one end of a cage and a blindfolded, nose-stopped individual at the other, it was noticed that the former moved to the end containing the latter. The blindfolded, nose-stopped snake was removed and its cloacal region carefully covered with adhesive tape and then covered with vaseline. When replaced in the cage it moved to within 4 cm. of the blindfolded one. The latter immediately moved forward to bring its body in contact with the taped snake. The blindfolded snake was then removed and a blindfolded tongueless individual substituted. This snake, like its predecessor, soon aggregated with the taped snake. The latter being both blindfolded and nose-plugged, moved about the cage aimlessly. When it came within 5 to 7 cm. of the blindfolded and tongueless snake the latter was stimulated to move toward the taped snake and aggregate with it.

The blindfolded and nose-plugged snake was next thoroughly washed with soap and water and its cloacal region sealed as before with vaseline. The experiments with the blindfolded and the blindfolded and tongueless *Storeria* were repeated with similar results. The washing had not removed the source of attraction because both blindfolded and blindfolded, tongueless snakes would seek out the taped snake. However, the attraction appeared to be weaker because there was considerable moving about before the snakes settled down to form an aggregation.

The blindfolded and nose-plugged snake was then removed and its entire body covered with a thin layer of vaseline. When replaced in the cage with the blindfolded and the blindfolded, tongueless snakes it failed to call forth the aggregation response in these snakes. An infiltrated specimen of *S. dekayi* was placed in the cage to serve as a basis of comparison. The blindfolded and the blindfolded, tongueless snakes showed no more interest in the vaselined snake than they did in the motionless infiltrated specimen.

The experiment was repeated with 3 blindfolded and nose-stopped *Storeria* which had been covered with vaseline. When an untreated *Storeria,* a blindfolded, nose-stopped snake and a blindfolded, tongueless snake were added to the cage there was no aggregation with the vaselined snakes. At the end of a 30-minute period the blindfolded, tongueless and the blindfolded, nose-stopped as well as the untreated *Storeria* had clustered into a single group while the 3 vaselined snakes were isolated in 3 different parts of the cage.

These experiments indicate that the cloacal glands of *Storeria* do not

produce the substances which serve as the basis of attraction during aggregation in the dark. The experiments with the vaselined snakes suggest that integument of the body is the source of these odorous substances. This seems the more remarkable in that there are no glands in the general integument of the body. However, the conclusion is in agreement with the findings of Noble (1936) that the body integument and not the cloacal glands leave a trail which aids snakes in seeking and identifying the opposite sex.

TRAILING EXPERIMENTS

In the preceding series of tests it has been concluded that the body integument and not the cloacal glands, leaves the trail by which snakes seek or find one another. In view of the above conclusions it seemed of importance to carry out a series of trailing experiments to determine the sense organs involved and to elucidate the nature of the stimulus.

The first series of experiments was carried out during the months of November and December 1933. A series of normal *S. dekayi* as well as a series of blindfolded snakes was used in this experiment, also two series in which the snakes were blindfolded and either tongueless or nose-stopped. Trails were made by rubbing the cloacal regions of the body of a snake of the same species over a smooth surface or by rubbing body integument exclusive of the cloacal region over the same surface. The sex of the trailing snake was recorded as well as the sex of the snake with which the trail was made. The experiments were carried out on gravel, concrete and Alberene stone surfaces. The experiments as recorded in Table 13 were all carried out on an Alberene stone surface 70 x 160 cm. The trail was made on exactly the same place and the trailing animal was started at the same place each time throughout the entire series. The table was cleaned with soap and water after each experiment. Table 13 gives the sex of the trailing animal, the sex of the snake with which the trail was scented and the time taken for each trailing animal to cover the trail.

It can be seen from the above table that there is no sexual attraction. A male *Storeria* will follow a male trail as well as a female trail and vice versa—the female will follow a female trail as well as a male trail. This series of experiments also shows that the snake with its sense of vision incapacitated reacts in a normal manner in following the scented trail. In the blindfolded series the reaction time is slightly less than in the untreated series. This is possibly because the experiment was carried out in a lighted room and snakes having their visual sense functional reacted to influences other than the trailing factor. ‚Nevertheless, it can be clearly noted from these results that olfaction is the chief sensory modality for finding and following or avoiding the trail.

Figure 9 shows the trails of 2 males started at various regions at AB and ending at region D on the trail AED, made by rubbing the body integument of

TABLE 13. The sense organs involved in trailing.

Series	Trials	Sex	Trail Scent	Reaction Time
U	5	Male	Male B	3 min. 10 sec.
U	5	Female	Male B	3 min.
U	4	Male	Female B	4 min. 10 sec.
U	3	Female	Female B	3 min. 40 sec.
U	8	Male	Male C	Negative
U	5	Male	Female C	Negative
U	3	Female	Female C	Negative
U	4	Female	Male C	Negative
B	5	Male	Male B	2 min. 20 sec.
B	4	Male	Female B	3 min. 12 sec.
B	3	Female	Male B	2 min. 50 sec.
B	6	Female	Female C	Negative
B	5	Male	Female C	Negative
BT.............	5	Male	Male B	3 min. 25 sec.
BT.............	5	Male	Female B	2 min. 30 sec.
BT...........	3	Female	Female B	3 min. 45 sec.
BT.............	5	Male	Male C	Negative
BT.............	4	Female	Male C	Negative
BN.............	6	Male	Male B	Negative
BN.............	7	Female	Female B	Negative
BN.............	3	Female	Male C	Negative
BN.............	4	Female	Female C	Negative

C designates scent from cloacal glands.   B designates scent from other body regions.

a male over the course. Figure 10 shows the same 2 males started at AB. In this case AED was again scented with body integument exclusive of the cloacal region while trail BEC was scented with cloacal gland secretion. This figure, as well as the results in the previous table, again substantiate the previous conclusions regarding the nature of the olfactory stimuli. The snakes not only fail to follow a cloacal scented trail, but tend to avoid it. In all cases the snakes failed to cross a trail scented with cloacal gland secretion.

In the next series of experiments a group of S. dekayi was collected from the Long Island region on April 16, 1934, and brought into the laboratory. They were placed in a refrigerator room and left there for a period of 24 hours at a temperature of 7° C. They were then placed in the usual type of cages having a layer of moist gravel on the bottom and placed in the greenhouse. These snakes showed active signs of courtship following the above procedure and were then used in the following series of trailing experiments. Since, in the previous series of experiments no sexual differentiation in respect to trailing could be established it was thought of sufficient importance to repeat the above experiments with sexually motivated snakes and to compare the trailing of these snakes with others which showed no sex responses.

Table 14 records the results as obtained with both male and female S. dekayi following a trail made by rubbing body integument on the substrata.

The trails were made over the same surface employed in the previous experiment and the time taken for sexually active *Storeria* may be compared with that recorded in Table 13.

From these results it can be seen that a courting male will follow an active female trail scent more rapidly than a non-courting male will follow a non-active female. This is illustrated by comparing the first series (Table 14) with the third "U series" in Table 13. During the breeding season a male will not follow or pay attention to the trail of another male. The

TABLE 14. Trailing experiments with sexually active *S. dekayi*.

*Trailing Snakes	Trials	Trail Scent	Reaction Time in Minutes
Male N	5	Female N	2.4
Male N	5	Female O	8.0
Male N	5	Female N and Female O	2.9 on Female N
†Male N	5	Female N and Female NC	2.7 on Female N
Male N	5	Male N	No Reaction
Male N	4	Male O	No Reaction
Male O	3	Female N	4.8
Male O	2	Female O	5.2
Male O	3	Male N	4.1
Male O	2	Male O	4.6
Female N	4	Female N	3.3
Female N	3	Female O	3.4
Female N	3	Female N and Female O	4.5 on Female N
Female N	5	Male N	4.2
Female O	3	Female N	4.1

*Snakes used for trailing — N, sexually active.
O, sexually inactive.
†NC, trail scent from cloacal gland of inactive female.

females do not react in any different manner than females during the winter months. The experiment with cloacal gland scent was repeated and it can be seen that here again this scent is avoided. In conclusion, it may be stated that normally, irrespective of the breeding season, there is some odorous substance given off by the integument of these snakes which attracts other members of the same species, and that during the breeding season this, or more probably another substance, is given off by the female which in turn attracts the male and enables the male to distinguish sex. The nature of this substance is as yet undetermined.

The recent experiments of Kahmann and others indicate that the chief function of the flickering tongue of snakes is to pick up odorous particles in the air and carry them to Jacobson's organ. Our experiments on trailing and aggregation described above clearly indicate the olfactory organs are more important receptors than Jacobson's organs in this behavior. Although a study of the feeding behavior of snakes lies beyond the scope of this paper, it seemed desirable for comparative reasons to obtain further information on the trailing habits of the species under consideration. We, therefore, induced

a series of *S. dekayi* and *T. sirtalis* to follow a food-scented trail. Figure 11 shows an outline of a soapstone surface, the continuous line being the food-scented trail and the broken line the distilled water trail of the control.

The food used was a preparation of earthworm extract made by grinding up earthworms and filtering off the liquid after a small quantity of water had been added to the crushed earthworms. This extract was placed on a marked trail as shown above and water containing no earthworm odor was placed on another trail as illustrated. The test snake was placed in region D at the beginning of the test and a sketch of each trail made. The time required to reach the end of the stone surface BC was recorded. The Alberene stone surface used throughout the experiment was 74 cm. in width and 366 cm. in length. The food trail as outlined in the above Figure 11 was therefore approximately 424 cm. in length. In each series of tests the food and water trails were reversed. This was done so as to eliminate any chance of a snake's developing place habits. We also employed a number of different snakes of each species in each series of tests.

Figure 11 shows the trail of a normal *Storeria* over the food-scented trail. The time required to cover the trail from D to C was 9.5 minutes. This series was repeated 10 times with normal, untreated *Storeria*. The results are recorded in Table 15. In all trials the snakes reacted positively to the scented trail and the average time required for the entire series was 9.9 minutes. If the above series is compared to the following series of untreated *T. sirtalis* it can be seen from Table 15 that while the reaction was positive in all cases the time required was nearly twice that of the above series of *Storeria*. Figure 12 shows the trail of an untreated *T. sirtalis*. The time taken to transverse the route CB is much longer than that for *Storeria* while the actual trail of the *T. sirtalis* is not proportionately extended. This shows that *T. sirtalis* is much slower in following and picking up the scent.

Table 15 shows that in the case of the tongueless and the blindfolded series no significant deviation from the untreated series was evident. However, in the nose-stopped series the time consumed was greatly increased (Fig. 13). This is particularly true of the *Storeria*. In the series in which Jacobson's organ was incapacitated the time required was again increased but not so much as in the nose-stopped series (Fig. 14). This, no doubt, shows the more important significance of the nose over the Jacobson's organ in finding a food trail. When both Jacobson's organ and the nostrils were incapacitated, no reaction was evident. The snakes moved around without any regard for the food-scented trail. Sometimes they refused to move from region AD while at other times they moved from AD to CD as in Figure 15, but showed no evidence of following any trail.

From the above experiments it may be concluded that neither the tongue nor Jacobson's organ is essential for finding food or following a food-scented

TABLE 15. Sense organs involved in the finding of food.

Series	Species	Trials	Reaction Percentage	Average Time in Minutes
U	S. dekayi	10	100	9.9
U	T. sirtalis	10	100	18.0
T	S. dekayi	15	100	12.1
T	T. sirtalis	10	100	16.6
B	S. dekayi	10	90	⎡0.6
B	T. sirtalis	10	100	20.2
N	S. dekayi	15	86	37.7
N	T. sirtalis	15	100	33.5
J	S. dekayi	15	93	19.0
J	T. sirtalis	10	90	21.0
BNT	S. dekayi	10	...	....
BNT	T. sirtalis	10	...	....
TJ	S. dekayi	15	100	16.0
TJ	T. sirtalis	15	93	24.0
TJN	S. dekayi	20	..	....
TJN	T. sirtalis	20	...	...
JN	S. dekayi	15	..	....
JN	T. sirtalis	15	...	....
TN	S. dekayi	15	...	....
TN	T. sirtalis	10	...	....

trail. The above function can be accomplished by the use of the olfactory organs alone. However, S. dekayi and T. sirtalis, having only the tongue and Jacobson's organ functioning, can follow the food-scented trail. The tongue alone, or Jacobson's organ alone, is inadequate in effectig a positive response to a food-scented trail. In brief, we may conclude that we have found very little evidence to support the views of Kahmann (1932). This is the more surprising in that Storeria and Thamnophis are closely related to the species of Natrix studied by him.

DISCUSSION

The most extensive aggregations of Storeria dekayi in the wild state are those taking place at the time of hibernation. The evidence presented above clearly indicates that the sensory-motor mechanisms bringing the snakes together at that time are the same as those which regulate the smaller aggregations of summer. A dropping temperature does not increase the magnitude of the aggregation response, but a snake which has been chilled moves into a warmer area when the temperature is sufficiently high to permit movement. This response brings scattered individuals into more favorable situations for

hibernations. The response to humidity is equally direct, the snakes seeking areas providing optimum conditions. When the temperature or humidity of an area deviates from the optimum the snakes tend to leave it for more favorable localities. They do not move out of this area at random, but follow the trails made by the skin of individuals of their own species. In October during both 1934 and 1935, we witnessed a movement of DeKay snakes across a street in the general direction of the hibernating area. This was on warm days (13 to 14° C.) following several colder ones when no snakes were visible. Most of the snakes were heading south and presumably along trails made by earlier arrivals.

This tendency of snakes to trail is merely a manifestation of the aggregation drive. When DeKay snakes are frightened their aggregation drive appears in its clearest form, but at other times when hunger, thirst, sex or other dispersing drives are dominant some tendency to aggregate remains. It is for this reason that the distribution of *Storeria* in any meadow or along any bank tends to be spotty.

The aggregation drive of *Storeria* and *Thamnophis* has a decided survival value. The normal response of these snakes to temperature or humidity gradients may bring them into favorable areas for wintering, but it is the tendency to trail which brings them in follow-the-leader fashion to the most suitable cavities.

During conditions of drought, the aggregation drive brings the snakes into contact with their kind with the result that less water is lost by evaporation through the skin. Aggregation also lowers the respiratory rate of these snakes conserving water which would be lost through the lungs. Allee (1931) has shown in a number of forms, particularly invertebrates, that aggregation has physiological advantages. Some of these advantages, particularly a lower metabolic rate, apply equally well to snakes (Clausen, 1934). Schuett (1933) reported a lower metabolic rate in fishes as the result of aggregation. In a later paper (Schuett, 1934) he finds that the earlier results were in error because of defective technique. Nevertheless he shows by a direct observational method that aggregation is beneficial in that it reduces activity. The aggregation drive of *Storeria* may be compared to the schooling drive of fishes, especially to that of those fishes which school only under adverse circumstances. Many of the cichlids when frightened, dash off in the same direction and form a compact group behind some shelter. Under unfavorable conditions of temperature and ionization these fishes also cluster together. The sensory components essential to hold the fish and the snake aggregates intact may differ. It has frequently been noted that fish schools such as those of the herring (Hesse and Doflein, 1914) or young catfish (Bowen, 1931) break up at night. Visual impulses therefore play as important a rôle in the formation of schools of fishes as in the aggregations

of snakes. But in the young catfish Bowen (1932) has shown that tactile impulses called forth by the reciprocal movements of the fish are also required for maintaining the school. In the snake the olfactory (or Jacobson's) organ must be properly stimulated if the aggregates are to continue. The sensory requirements in aggregating fishes and snakes may not be the same, but in both groups the tendency to cluster when frightened or when subjected to adverse conditions remains.

The hibernating den of *Storeria* and *Thamnophis* may be restricted to a single cavity or it may be widely scattered along many subterranean channels. Although most snake dens are assumed to be restricted to single cavities further work may show that the diffuse den of *Storeria* and *Thamnophis* is equally characteristic of other species. During January, 1933, we excavated a den of *Crotalus horridus* and *Agkistrodon mokasen* near Stony Point, N. Y. No less than 8 specimens of the former species and 21 of the latter were taken from an area 12 yards square. Two of each of the above species were also removed from a region 12 yards from the above area. The snakes were found singly or in groups of 2 and 3 scattered along crevices approximately 4 feet from the surface. Two *Coluber constrictor* were taken in this same area but they were not in cavities occupied by the other two species. Just as *Thamnophis* and *Storeria* were attracted to the same areas late in the fall primarily by the warmth of these localities, so the physical conditions had presumably attracted the black snakes, copperheads and rattlers to the same hillside. When few cavities are available on a particular hillside two species may hibernate together, but there is a distinct tendency at least in the species studied above for each species to seek isolation from other species.

Snakes in following trails make use of their tongues to carry the odors to the Jacobson's organs as Baumann (1929), Kahmann (1932), and others have described. Some lizards such as most Teiidae have long bifid tongues which are frequently flickered. Noble and Kumpf (1936) have shown that in spite of this important distance receptor the teiid lizard they studied still depended primarily upon its olfactory organs when seeking food. Similarly we find that in both food-seeking and companion-seeking activity, *Storeria* and *Thamnophis* are guided more by stimulations of the olfactory than by those of their Jacobson's organs.

SUMMARY

1. *Storeria dekayi* exhibits a well marked tendency to aggregate with numbers of its own species. This tendency becomes more pronounced by disturbing factors. It is present to a certain degree in some other snakes such as *Thamnophis sirtalis* and *T. butleri.*

2. Aggregation in *S. dekayi* occurs throughout the entire year with the

exclusion of the time during which gestation occurs. At this time the females are found isolated.

3. Aggregation is beneficial in that it reduces water loss. As the temperature increases the aggregation response becomes more and more beneficial.

4. There is considerable variation between species as to effectiveness of aggregation under similar conditions. This difference is correlated with the habitat preferences of the species.

5. There is a direct correlation between weight decrease and respiratory increase under isolated and aggregated conditions. Desiccation tends to reduce both weight and respiratory rate.

6. The typical aggregation response of *S. dekayi* occurs when the humidity lies between 20 and 45 per cent. The sense organs involved in the response to humidity gradients are not those involved in aggregation.

7. Aggregation in *S. dekayi* occurs normally within a more or less definite temperature range (21° to 31° C.). *T. butleri* forms typical aggregates at higher temperatures than the optimum for *S. dekayi*.

8. Vision is the primary sensory modality which enters into the aggregation response. Olfaction plays a secondary rôle, while the tongue plays little or no part in the reaction.

9. DeKay snakes are attracted by moving objects of small size. A motionless snake will not serve as a source of attraction. Color appears to have little significance.

10. Species identification is accomplished chiefly by the olfactory sense while vision enters into the response secondarily. The tongue itself plays no part in species identification.

11. The secretion of the cloacal glands does not attract. The integumental covering of the body is the source of odorous substances which serve in one case as an attraction to other individuals of the same species and in the other case to individuals of the opposite sex.

12. The olfactory organs alone are adequate sensory mechanism for food trailing in *S. dekayi* and *T. sirtalis*. The tongue and Jacobson's organs in combination make trailing possible, but either one of these structures alone is inadequate.

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THE COMPOSITION AND DYNAMICS OF A BEECH-MAPLE CLIMAX COMMUNITY[1]

By

ARTHUR B. WILLIAMS

Cleveland Museum of Natural History

CONTENTS

THE COMPOSITION AND DYNAMICS OF A
BEECH-MAPLE CLIMAX COMMUNITY

INTRODUCTION

The approach in this study is to the biotic community as a whole. It is sought to determine both its plant and animal content; the number and abundance of species; their relations to each other and to the community as a whole; seasonal and yearly variations in numbers and activities; territorial relations; food relations; the stage of succession represented; changes now going on; environmental conditions, including soil and climatic factors; and the effect of these upon the community.

Special emphasis is laid upon the vertebrates and the major plant forms. While it has not been possible to treat the invertebrate life as fully as the plants and vertebrates, some invertebrates have been noted, and are included in this paper.

The writer desires here to acknowledge his indebtedness and to express his appreciation to the Cleveland Metropolitan Park Board for the opportunity afforded for this study within the Cleveland Metropolitan Park System, and for many courtesies extended by park officials; to the Cleveland Museum of Natural History for making this study possible as a piece of research in connection with its program, and to Mr. Harold L. Madison, Director of the Museum, for encouragement in it; to Dr. J. Paul Visscher, Chairman of the Department of Biology of Western Reserve University, for the privilege of coördinating a study of this kind with the regular work of the Department, and especially to Dr. S. C. Kendeigh, of the Department of Biology of Western Reserve University, for his many helpful suggestions and criticisms during the progress of the work and the preparation of this paper.

The writer's thanks are also due to Dr. Addie E. Piehl of the Department of Biology of Western Reserve University for aid in identifying mosses, lichens, and algae; and to Mr. Henry M. Beardslee, of North Perry, Ohio, for similar aid in identifying fungi. To Mr. B. P. Bole, Jr., mammologist of the Cleveland Museum of Natural History, and to Dr. Harry C. Oberholzer, of the United States Biological Survey, the writer is indebted for checking the lists of mammals and of birds, respectively, with special reference to subspecies names. To Mr. Arthur B. Fuller, of the Cleveland Museum of Natural History, to whose expert marksmanship the collection of all of the bats taken in the area is due (for which special permission was given by the Park Board for the purposes of this study), the writer is also indebted. To Mr. Philip Moulthrop, also of the Cleve-

land Museum of Natural History, the writer is indebted for much help in the collection of small mammals.

It is not maintained that this study is now complete. In a sense it might be carried on indefinitely and never be complete. It seems desirable, however, at this time to make available the data thus far collected and to report the findings.

The beech-maple forest (Fagus-Acer association) is an important ecological division of the deciduous forest formation, which formation at the coming of the white man occupied so large a part of the northeastern United States and southern Canada. The deciduous forest has been described by Transeau (1905), Harshberger (1911), Frothingham (1915), Clements (1916), Livingston and Shreve (1921), Shantz and Zon (1924), and Weaver and Clements (1929). Weaver and Clements give the limits of the deciduous forest formation as running on the north from central Minnesota along the south shore of Lake Superior eastward to southwestern Quebec and southern Maine, thence stretching southward into central Georgia, southern Louisiana, and eastern Texas. The same authors regard the beech-maple forest as the "typical association" of the deciduous forest formation, "characterizing its more humid and cooler northern and eastern portions."

The plant structure of the beech-maple association has been studied in detail in southern Michigan by Quick (1923) and by Cain (1935), in northern Michigan by Gleason (1924), and in Indiana by Esten (1932). In Ohio the beech-maple association is emphasized by Sampson (1927) as one of the four primary plant communities in the state on the basis of area covered. Sears (1925), attempting to reconstruct the picture of the natural vegetation of Ohio before the advent of the white man noted that beech, unmixed with oak or ash, was practically limited to the glaciated region of the state. References to the occurrence of both beech and sugar maple throughout their range will be found in the Naturalists' Guide to the Americas, edited by Shelford (1926).

Hemlock is recognized as a frequent constituent of the beech-maple association (Gleason 1924, Weaver and Clements 1929). The hemlock forest has been described by Lutz (1930) and the environmental requirements of hemlock studied by Moore, Richards, Gleason and Stout (1924).

The animal content of the forest, the relationships between plants and animals, and the consideration of the biotic community as such have not thus far been given the consideration accorded to the plant constituents of the community. Important contributions have been made in this country by Adams (1906), Shelford (1913), and Chapman (1931); and in England by Elton (1927, 1930). The mammals of a beech-maple forest in Michigan have been listed by Dice (1920), and an ecological survey of Isle Royale conducted by Adams (1909) included a study of animals found there.

The insect life of an elm-maple forest in Illinois has been studied in detail by Weese (1924), and much the same thing has been accomplished by Blake (1926), working on Mount Katahdin in Maine. A study of the biotic communities of the aspen parklands of central Canada was made by Bird (1930). Shelford and Olsen (1935) have pointed out the relation which animals may have to plant communities as indicators, and maintain that plants and animals are inseparably united in the structure of any community. Much painstaking labor has been devoted to the study of various phases of animal ecology by numerous workers, but there is little in the literature that treats of forest communities as biotic units.

DESCRIPTION OF AREA STUDIED

LOCATION AND PHYSIOGRAPHY

To the northeast of Cleveland, Ohio, and some 16 miles from the city limits, lies the tract of land known as the North Chagrin Reservation of the Cleveland metropolitan park system. It contains 1,201 acres (486.04 hectares), and is roughly rectangular in shape, being approximately a mile and a half (2.41 kilometers) square (Board of Park Commissioners, Report 1932-1933). It lies between parallels 41° 33′ and 41° 35′ north latitude.

The reservation occupies a position at the extreme edge of Appalachian Plateau, as the Portage Escarpment which limits the plateau in this region is represented by the high bluffs of the Chagrin River valley which are a part of the area. The location is well within the boundaries of the advance of the ice sheets of Pleistocene times (Cushing, Leverett, and Van Horn 1931). Lake Erie is distant about 5 miles (8.04 kilometers) in a direct line toward the northwest.

Within the reservation the land slopes gently toward the east for about a mile (1.6 kilometers), where it drops steeply almost to the level of the river. This bluff which marks the border of the valley is deeply and frequently cut by short gullies and ravines only a few of which are extensive enough to carry water all the year. The United States topographical survey map (Mentor Quadrangle) shows the difference in level between the western margin of the reservation and the river to be 220 feet (67.05 meters).

The particular area chosen for this study lies along the southern boundary of the North Chagrin Reservation. It is approximately 65 acres (26.3 hectares) in extent, is entirely wooded, and includes some of the characteristic gullies, ravines, and bluffs of the locality. It does not include any of the river bottom or lower lands. It slopes toward the northeast from 860 feet (262.12 meters) to 760 feet (231.64 meters) above sea level. In outline it is somewhat irregular, because of the nature of the ground, except at its southern and western limits. It is traversed by several foot-trails and
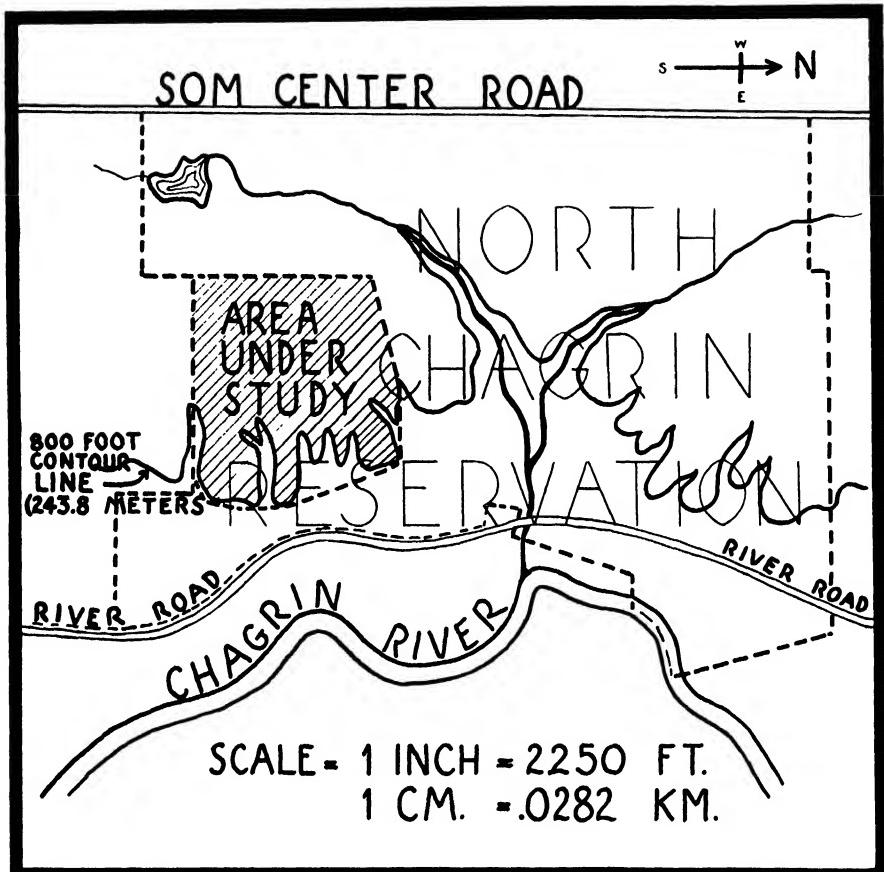
FIG. 1. Map of North Chagrin Reservation showing location of area under study.

bridle-paths which greatly facilitate quiet and easy access to all of its parts. Reference to Figure 1 will give an idea of the topography of the area and of its relation to the entire North Chagrin Reservation. It should be noted that the reservation is not an isolated piece of forest land. While to the west the country is occupied by farms, the adjoining land to the north and south and across the river to the east is largely of the same character as that of the reservation itself.

GEOLOGY AND SOIL

The geological formation immediately underlying the surface soils is that known as the Cleveland Shale. This is a sedimentary rock apparently composed of consolidated black mud (Cushing, Leverett, and Van Horn 1931). Upon this bed-rock of shale a layer of soil of glacial origin known as the Volusia Clay Loam has been deposited. Coffey and Rice (1912), describing this soil, say: "As a general rule, both soil and subsoil are markedly

deficient in lime carbonate, and will redden litmus paper quickly. The Volusia series is derived from glacial deposits of shale and sandstone material which covers the northeastern section of Ohio." The Volusia Clay Loam is a poorly drained soil, and not among the more productive soils of the State. The presence of beech trees is said to be characteristic of the Volusia series. Over the clay loam above described there has been built up a layer of humus of a loose and spongy character from 1 to 4 inches (2.54 to 10.16 cm.) in depth. The clay soil beneath the humus is not more than from 4 to 9 inches (10.16 to 22.86 cm.) deep, but it is friable and porous as compared with the subsoil, which is of dense yellow clay.

DRAINAGE

Because of the heavy quality of the underlying sub-soil, standing water, in hollows, after rains or melting snows, is of common occurrence on the more level parts of the area. Depressions left by the uprooting of large trees will sometimes contain water most of the year if precipitation is fairly regular. In winter and spring the woods of the higher or more westerly part of the area are always wet. Aside from such water as may collect in depressions or pockets, the run-off of excess water is rapid. Within the area there are no constant streams, the waterways with one exception being short and the gradient steep. One waterway, having its collecting basin in the open fields outside the area, and traversing its higher portion in more leisurely fashion, does not become entirely dry except after periods of prolonged drought.

CLIMATE

The close proximity of Lake Erie may be considered as a factor modifying to some extent the climate of the region. In general, as has often been pointed out, temperatures do not rise so high nor fall so low near the lake as they do farther inland. The lake also is often responsible for a condition of cloudiness that cuts down very appreciably the amount of available sunshine (Moseley 1897).

In order to secure positive information as to the factors of temperature, humidity, and precipitation within the area, four stations were established and their operation begun on January 1, 1932. Two of these stations, designated as "A" and "B," were located in beech maple environment. The other two, designated as "C" and "D," were located in beech-hemlock environment. At Station A a hygrothermograph giving continuous records of temperature and relative humidity was installed in a wooden shelter resting on the ground. A rain gauge, by means of which precipitation over a circular area 3 inches (7.62 cm.) in diameter may be measured in hundredths of an inch, was located here. At Stations B, C, and D, maximum and minimum thermometers and rain gauges similar to that at Station A were in-

stalled. The thermometers were secured to the north sides of large trees about 5 feet (1.52 meters) from the ground, and the rain gauges located beneath the same trees from 6 to 10 feet (1.82 to 3.04 meters) from their bases. Readings from all instruments were taken with regularity weekly, and the operation of the hygrothermograph regularly checked as to temperature with a tested thermometer, and as to relative humidity with a cog psychrometer. The thermometers were compared at different temperatures, and their readings found to be in agreement. Their accuracy was also checked with a standard thermometer.

TEMPERATURE

Figure 2 shows the mean temperature by weeks, on the basis of hourly readings, at Station A for the year 1932. To this has been added the records of mean temperature for the same weeks as recorded by the Cleveland Weather Bureau, and also the curve of normal temperature for Cleveland It will be noted that the means for Cleveland follow closely the fluctuations recorded at North Chagrin. It is thus possible to construct a table of corrections for the Cleveland figures which may be used for further temperature studies at North Chagrin. Table 1 shows these corrections. It is apparent that the appearance of the leaves on the trees, and the development of a full and dense cover of foliage, which takes place from the middle of May to the middle of June is a definite factor in modifying temperatures in
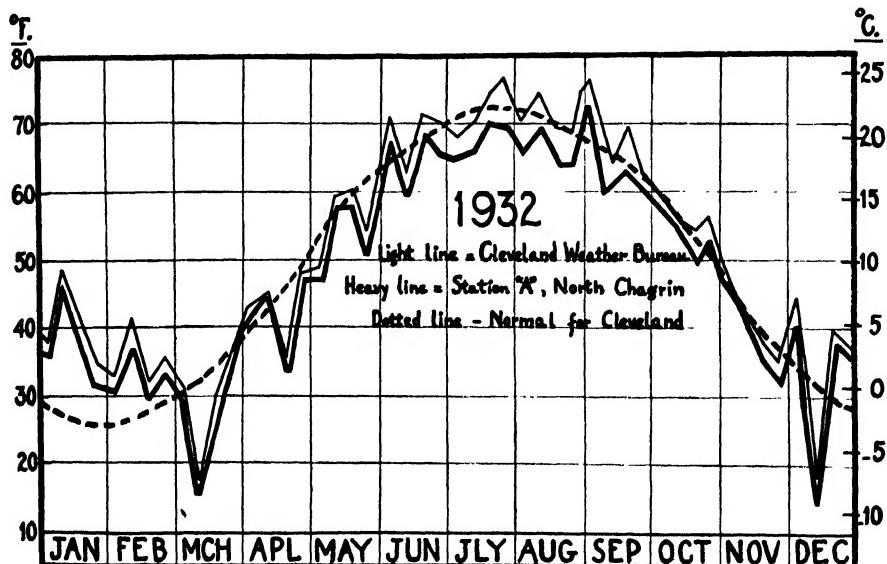
Fig. 2. Mean temperature by weeks on the basis of hourly readings at station "A," 1932, with mean temperature recorded for the same period by the Cleveland Weather Bureau. Curve of normal temperature for Cleveland.
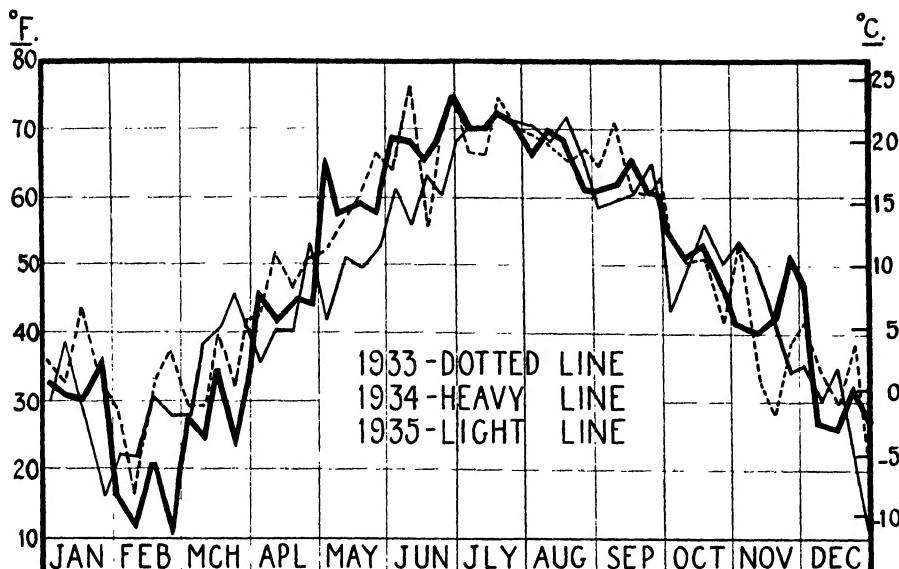
FIG. 3. Weekly mean temperature at North Chagrin, 1933, 1934, and 1935, from Cleveland Weather Bureau figures corrected in accordance with table 1.

the beech-maple forest. The Cleveland station of the U. S. Weather Bureau gives 200 days as the length of the growing season in this locality.

By the use of the correction figures (Table 1) the mean weekly temperatures at North Chagrin for the years 1933, 1934, and 1935 are shown not to be greatly different from those of 1932 (Fig. 3). Differences in temperatures recorded at the 4 stations were not great enough to be considered especially significant. After the middle of May when the leaves were on the trees there was little or no difference in the minima and but slight difference in

TABLE 1. Differences between temperatures at Cleveland and at North Chagrin, 1932, averaged for each month, and figures used for correcting Cleveland temperature records to show conditions at North Chagrin. (1° F. = 0.56° C.).

Month	Weekly Mean		Weekly Maximum		Weekly Minimum	
	Actual Difference	Correction Figure	Actual Difference	Correction Figure	Actual Difference	Correction Figure
January........	−2°F.	—2°	—2°F.	-3°	—1°F.	—1°
February..	—3	--2	—5	—3	—2	—1
March....	—2	—2	—4	—3	--4	—4
April..........	—1	--2	0	—3	—3	—4
May....... ...	—2	—2	---1	—3	—4	—4
June..	—4	—4	-3	—3	—6	—6
July........ .	--5	—5	—5	---5	—4	—6
August........	—5	—5	—6	-6	—6	—6
September......	—4	--4	—6	-6	—9	—6
October........	—3	--3	—4	—4	—3	—3
November......	--2	—2	—3	—4	—3	—3
December......	--2	—2	---4	—4	—1	—1

the maxima of all stations, 4° being the greatest divergence recorded. It may be said, then, that temperature in the area at five feet above the ground is practically uniform throughout, whether in beech-maple or in beech-hemlock environment, except as affected in minor ways by exposure or shelter.

RELATIVE HUMIDITY

Figure 4 shows the weekly means of the records of relative humidity on the basis of hourly readings at Station A for the year 1932. The mean relative humidity for the year was 83.3 per cent. When a comparison by weeks is made it appears that with few exceptions the amount of relative humidity was generally between 75 and 90 per cent. Records of many hours showed frequent periods of 100 per cent. A notable exception occurred during the latter part of April, a time of low precipitation, when great extremes of humidity were recorded daily, the record fluctuating between 16 and 100 per cent.
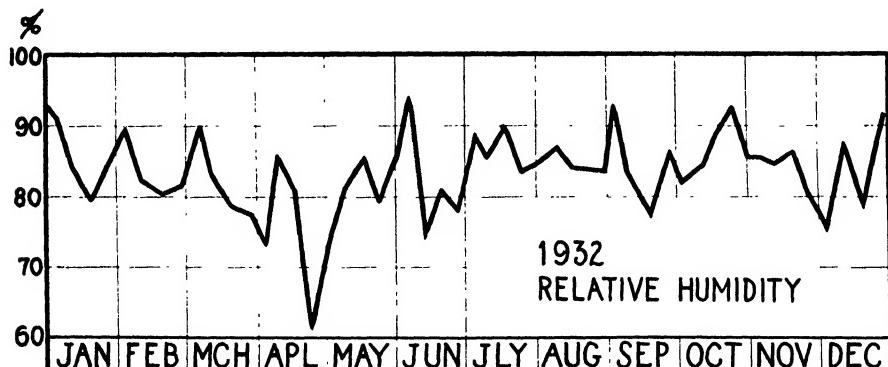
Fig. 4. Mean relative humidity by weeks on the basis of hourly readings station "A," 1932.

PRECIPITATION

Records of amount of precipitation were obtained weekly during 1932 at all 4 stations. The individual instruments at times varied somewhat as to amount of water collected, but in the long run they approximated fairly closely (Table 2).

TABLE 2. Total precipitation at 4 stations: January 1 to December 31, 1932.

Station A — beech-maple   — 31.70 inches (80.52 cm.)
Station B — beech-maple   — 32.41 inches (83.32 cm.)
Station C — beech-hemlock — 29.23 inches (74.24 cm.)
Station D — beech-hemlock — 29.11 inches (73.94 cm.)

If the records of the two stations in beech-maple environment be averaged, and compared with the average of the two stations in beech-hemlock environment, it appears that the hemlocks received 2.88 inches (7.31 cm.) less water about their roots during the year than did the deciduous trees.

Since so little variation in precipitation was shown between the stations, the taking of further precipitation records was continued at Station B only. The records at this station by months for the 4 years of this study is shown in Figure 5, use being made of the diagrammatic method first introduced by Transeau in 1931 (Cain 1932). A study of these precipitation patterns discloses the fact that in 1932, during the growing season and immediately before, precipitation was very light, and that again in 1933 conditions during the growing season were marked by a deficiency of moisture. In fact, such rain as did fall in the summer of 1933 was concentrated in a few downpours which, because of the rapid run-off and speedy evaporation, was very ineffective, hardly reaching the soil beneath the forest litter to any great extent.

The year 1934, however, proved to be one in which precipitation, though deficient in May, was above normal in the summer and autumn, although this was the year of the great drought in other parts of the country. Because this record seems unusual it is fortunate that records of precipitation are available for the summer and early autumn of this year from the farm of Mr. B. P. Bole at Kirtland Hills, about 6 miles (9.65 kilometers) to the northeast, as a check upon the North Chagrin records. As a further check 2 additional rain gauges were operated in the spring of 1935 on either side of the North Chagrin instrument and about 10 feet (3 meters) away from it. Over a period of 4 weeks all three instruments were found to be in accord. For purposes of comparison the Bole farm records and those of the Cleveland Weather Bureau for 1934, as well as the normal precipitation for Cleveland, are included in Figure 5. As a matter of general observation it may be said that weather conditions at Cleveland and at North Chagrin are frequently not the same.

WIND

That the forest is responsible in many ways for its own micro-climate is strikingly shown in the way in which the movement of wind within its borders is modified by the presence of trees and other plants both in summer and in winter.

Toward the west the edge of the forest under study is bordered by an open field, and so presents an unbroken front to the full force of the wind from this direction. At this point, readings with an anemometer of the "windmill" type, measuring the velocity of the wind in feet, were taken over periods of 5 minutes each, first outside the forest, to measure the force of the wind at this point, and at each succeeding 100 feet (30.48 meters) within the forest, following the direction of the wind, until a point 1,000 feet (304.8 meters) from the edge was reached. The velocity of the wind at the outside was then again measured, and the average of this, and the first outside measurement taken as the velocity of the wind during the hour or more consumed in taking all of the records. Six such
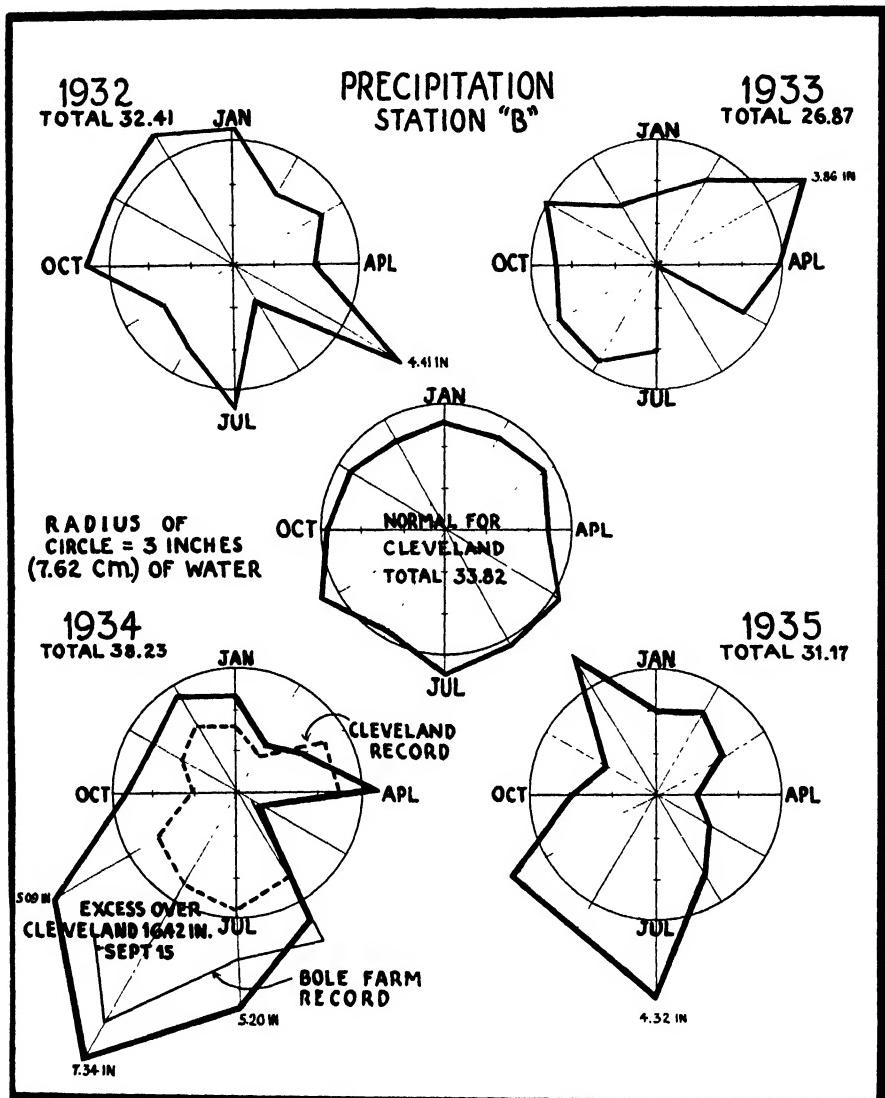
FIG. 5. Precipitation by months, station "B," 1932, 1933, 1934, and 1935, with Bole Farm records and Cleveland records for 1934, and normal for Cleveland.

complete records were obtained at various times and under various conditions when the trees were bare of foliage, and five complete records when the trees were in full leaf. Table 3 shows the amount of decrease in velocity after reaching the 800-foot mark. Records are reduced to feet per minute.

Reduced to percentages of decreased velocity from the forest edge inward, the results of these records are given in Figure 6. The records from the 700-foot point and further were usually of light and shifting air cur-

TABLE 3. Effect of forest on wind velocity.
(records in feet per minute)

Trees Without Leaves			Trees With Leaves		
Record	Average velocity in open	Average velocity 800-1000 ft.	Record	Average velocity in open	Average velocity 800-1000 ft.
1.	862 f.p.m.	161 f.p.m.	1.	763 f.p.m.	47 f.p.m.
2.	826	168	2.	573	22
3.	671	111	3.	481	27
4.	615	172	4.	343	23
5.	495	175	5.	284	64
6.	339	159	.		

NOTE: 100 feet = 30.48 meters.

rents. Several readings taken further within the forest showed essentially the same conditions. Comparing summer and winter conditions it appears that there is from 13 to 20 per cent more air in motion near the ground in winter than in summer.

SUNSHINE

Figure 7 shows the possible number of hours of sunshine by months for Cleveland, and also the actual number of hours of sunshine for the year 1932. For purposes of comparison the curve of the normal number of hours of sunshine for Cleveland is included. It is apparent that the total amount of cloudiness during the year is very considerable. Even though there were actually more hours of sunshine than normal in 1932 for 8 months out of 12, the actual number of hours of sunshine for the year were only 56 per cent of the possible number—the normal being 52 per cent. During the winter months, December, January, and February, the normal proportion of sunshine sinks to 24, 29, and 35 per cent of the possible number of hours.

While no measurements of light intensities were made, it should be noted that the beech-maple-hemlock forest is a dark forest in summer. One of the first things of which one becomes conscious upon entering this forest on a bright summer day, is of the great decrease of light intensity. The eyes need to become adjusted to this condition before much can be seen. The writer has frequently made exposures of 15 seconds duration on photographic film in order to get good pictures within the forest on days when the summer sun was shining brightly outside. Using the same aperture, lens, and film in the open on such a day would have necessitated an exposure of one-fiftieth of a second. Although this is by no means an exact measurement, it does indicate that light within the forest is one-seven-hundred-and-fiftieth as effective on photographic film in midsummer as it is outside the forest at the same time and otherwise under the same conditions.

PER CENT
OF DECREASE

NOTE :— 100 FEET = 30.4 METERS
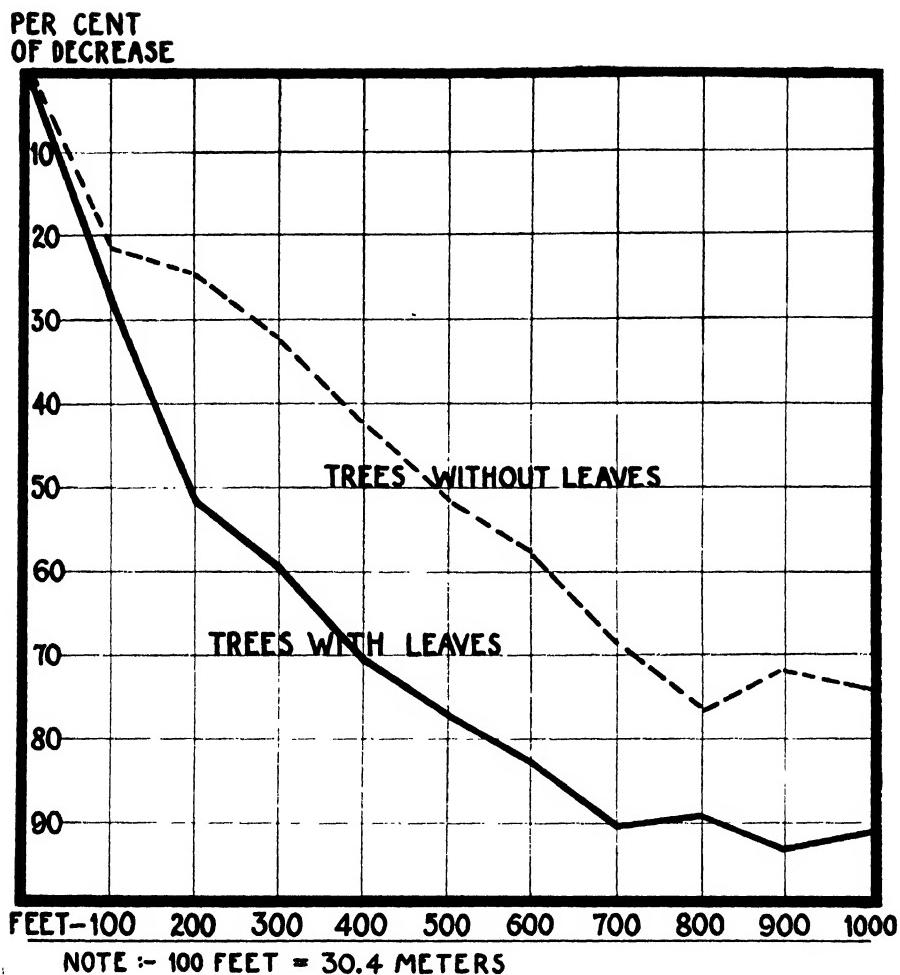
FIG. 6. Decrease in velocity of wind from forest edge inward in summer (heavy line) and winter (dotted line).

EVAPORATION RATE

During the summer of 1934 an attempt was made to secure data on the rate of evaporation of moisture, both in the forest, and in the open just outside the woods to the west. For this purpose standardized Livingston porous clay bulb atmometers were used, evaporating distilled water only. Although a group of three instruments were run in the woods, so that readings might be averaged, continual interference with the bulbs by gray squirrels, and the growth of protococcus on the bulbs at times, reduced the number of available instruments often to two, and sometimes to one. There were also two short periods when all instruments in the woods were out of
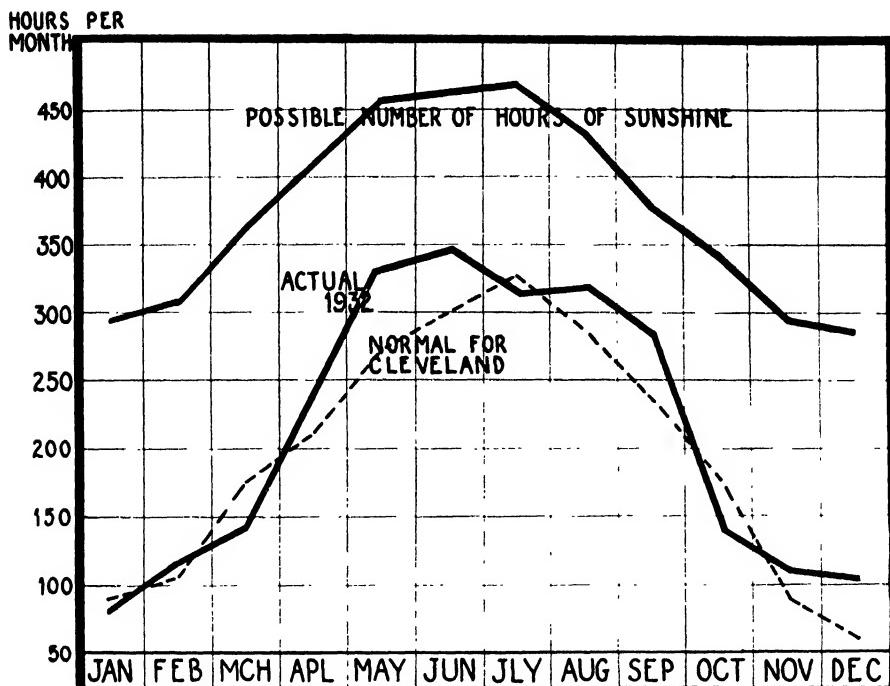
FIG. 7. Possible and actual number of hours of sunshine for Cleveland in 1932, and normal for Cleveland.

commission due to these causes. The one instrument in the open field ran continuously without interruption from August 1 to October 15 when the bulb was shattered by freezing. To get some idea of winter conditions, readings were taken twice over short periods in November and January when the temperature was above freezing. Table 4 gives the data obtained from these instruments.

The rate of evaporation is apparently affected greatly by various atmospheric conditions. Wind greatly increases it. Precipitation in summer and freezing in winter slows it up. High temperature with dryness is conducive to a high evaporation rate. The effect of the forest in reducing the rate of evaporation within its borders, as compared with conditions in the open, is striking, showing an average difference of 55.2 per cent in summer when the leaves are on the trees, and of 38 per cent in winter when the forest is more exposed to the influence of wind.

SUMMARY OF CLIMATIC DATA

From the data gathered over the four-year period of this study, the climate of the area may be summarized by saying that temperatures are not extreme, varying from -13° F. (-25° C.) in winter to 96° F (35.5° C.)

TABLE 4. Evaporation rates at approximately 12 inches (0.304 m.) above ground.

Date—*1934*	Open field. Rate of evaporation in cc. per hour	Beech-maple. Rate of evaporation in cc. per hour	Per cent of decrease from open to forest	Weather conditions
June 1 – 4..	.....	0.835	....	very dry
4 – 11..	.....	0.713	....	very dry
11 – 25..	.....	0.524	....	wet
25 – 2..	.....	0.402	....	very wet
July 2 – 9..	.....	0.404	....	very wet
9 – 16..	.....	0.271	....	very wet
August 1 – 6..	0.940	0.350	62.8	very wet
6 – 13..	0.807	0.285	64.7	very wet
13 – 22..	0.740	No record	....	very wet
22 – 27..	0.760	0.270	64.5	very wet
27 – 1..	0.610	0.255	58.2	wet
September 1 – 10..	0.497	0.275	44.7	wet
10 – 17..	0.287	0.152	47.1	wet
17 – 24..	0.520	0.231	35.6	wet
24 – 1..	0.428	0.223	47.9	wet
October 1 – 8..	0.619	0.180	71.0	very wet
8 – 15..	0.481	0.307	36.2 (leaves falling) – dry
November 24 – 26..	1.137	0.757	33.5 (heavy wind) —dry
1935				
January 6 – 7..	0.402	0.231	42.6 (ground frozen)

Average evaporation in forest, June 1 to October 15, — 0.355 cc. per hour per instrument.

in summer; that it may be subject to unseasonable weather, but that for the most part temperatures are within closer limits; that relative humidity is high, for most of the time ranging between 75 and 90 per cent; that precipitation is rather uniform throughout the year, averaging 2.84 inches (7.21 cm.) per month, or 31.62 inches (80.31 cm.) per year for the period of this study; that for 52 per cent of the time when sunshine is possible the sky is overcast; that the force of the wind is ordinarily so tempered by the trunks and branches of the trees in winter, and the addition of their foliage mass in summer, as to make wind disturbances rare throughout its lower levels; that the rate of evaporation is reduced within the forest from 47.1 to 64.7 per cent in summer to from 33 to 42.6 per cent in winter, as compared with the open field at its western edge.

HISTORY OF THE AREA STUDIED

The former Indian occupation of this region is well attested by the collections of flint and stone implements assembled over a period of years by Mr. Ray Parker and Mr. Carl Scheuring whose farms are located close to the area on the southwest. The forest of the area, says Mr. A. C. Keesler, who has lived all his life nearby, has always been a beech woods. The large stumps, well advanced in decay, seen occasionally in the woods, he says represent a cutting made when he was a boy of about 14 (1871), when some large oak, hickory and tulip trees were taken out for lumber. Ap-

parently the particular portion of the area in which our interest centers has suffered little from major disturbances for a long time. There is no evidence of serious fire, either in the place itself, or in the memories of those who, like Mr. Keesler, have a long family tradition associated with the place.

In 1925, 1926, and 1927, the Cleveland Metropolitan Park Board acquired practically all of the 1,201 acres (486.04 hectares) now known as the North Chagrin Reservation, and containing the area under study. Since that time all wild life within the boundaries of the reservation, including both plants and animals, has been under complete protection, no hunting, or other disturbance of natural conditions having been allowed. The policy of the Park Board has been that of conserving natural conditions as far as possible. Picnic grounds and playgrounds are located outside the forested areas. Foot-trails give access to the forest, but there has as yet been little straying from the trails on the part of visitors. No picnic parties are allowed within the woods. One bridle-path crosses the area, and another skirts its western edge. Two uniformed guards regularly patrol the entire reservation to see that park regulations are respected.

CHARACTER OF THE FOREST

PLANT CONSTITUTION

TREES

In 1932 the writer had recourse to the familiar quadrat method of determining the abundance and distribution of trees and shrubs throughout the area, but as increasing familiarity with the forest was gained it became apparent that the results obtained by the quadrat method were far from satisfactory, and this method was abandoned. Instead, during the winters of 1933-34 and 1934-35, all of the larger trees of the area were measured, and their approximate location charted on individual maps for each species. Measurements were made by tape giving the circumference breast high in inches, and only trees of 30 inches (76.2 cm.) or over in circumference, or slightly over 9.5 inches (24.13 cm.) in diameter, were thus measured and their location charted. Later, a count of all trees of each species was made, section by section, but without the use of quadrats or other measured areas. In this count an effort was made to include all trees down to the 3.5 inch (8.9 cm.) diameter class, the size being judged by eye. While the figures thus obtained are doubtless subject to some error the writer believes them to be substantially in accord with the facts.

On the basis of these counts and maps (Figs. 9 and 10) it appears that there exist 4 major vegetational divisions within the area (Fig. 8) which may be designated as follows:

(1) *The spurs of the eastern edge of the area.* Here occurs a forest
mictium including beech, hemlock, red oak, and chestnut, as dominants, to-
gether with a relatively large proportion of other species. Chestnut is as-
signed its position on the basis of large standing trees, though at the present
time none are living. It was so recently an important member of this com-
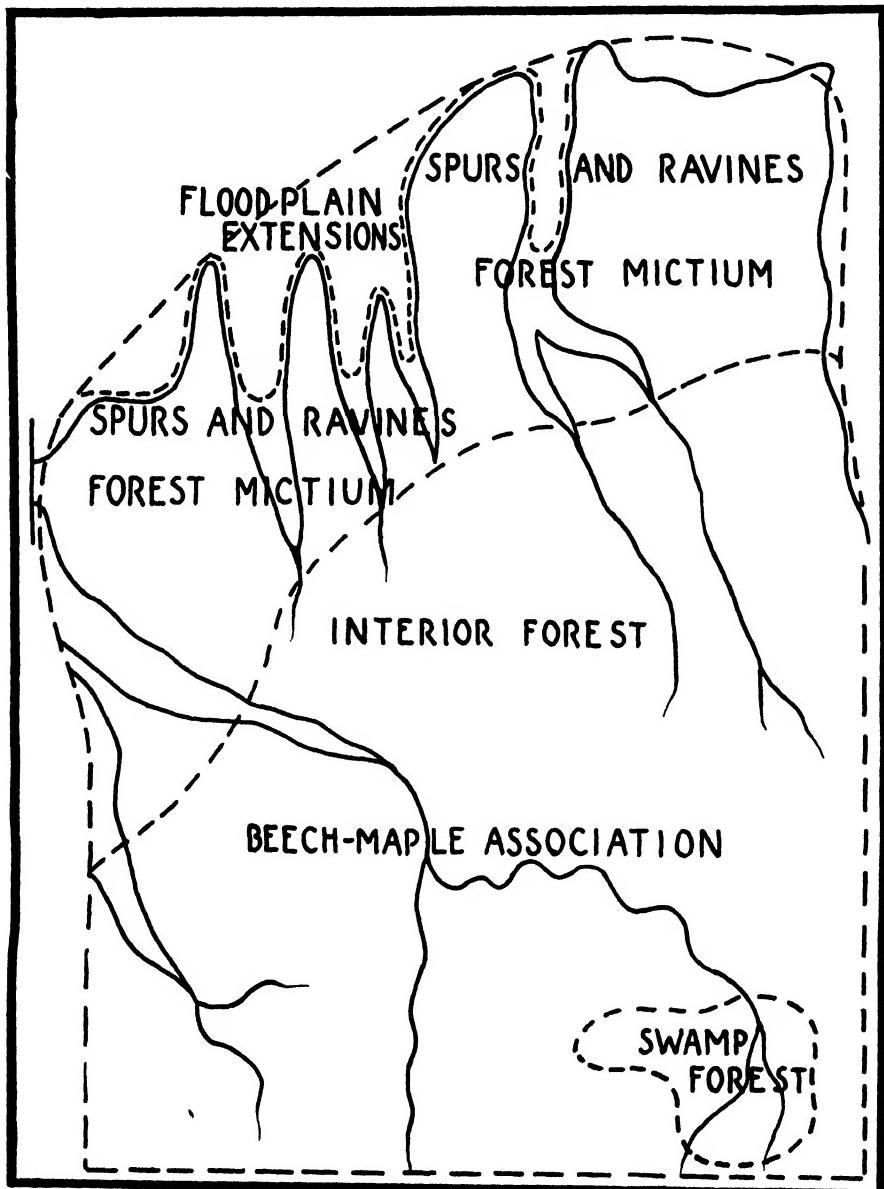
FIG. 8. Major vegetational divisions of the area under study.

munity that it seems desirable here and elsewhere in this study to recognize its former significance.

(2) *The ravines between the spurs.* In the deeper ravines an excess of moisture is always present. Here herbaceous vegetation prolongs its sea-
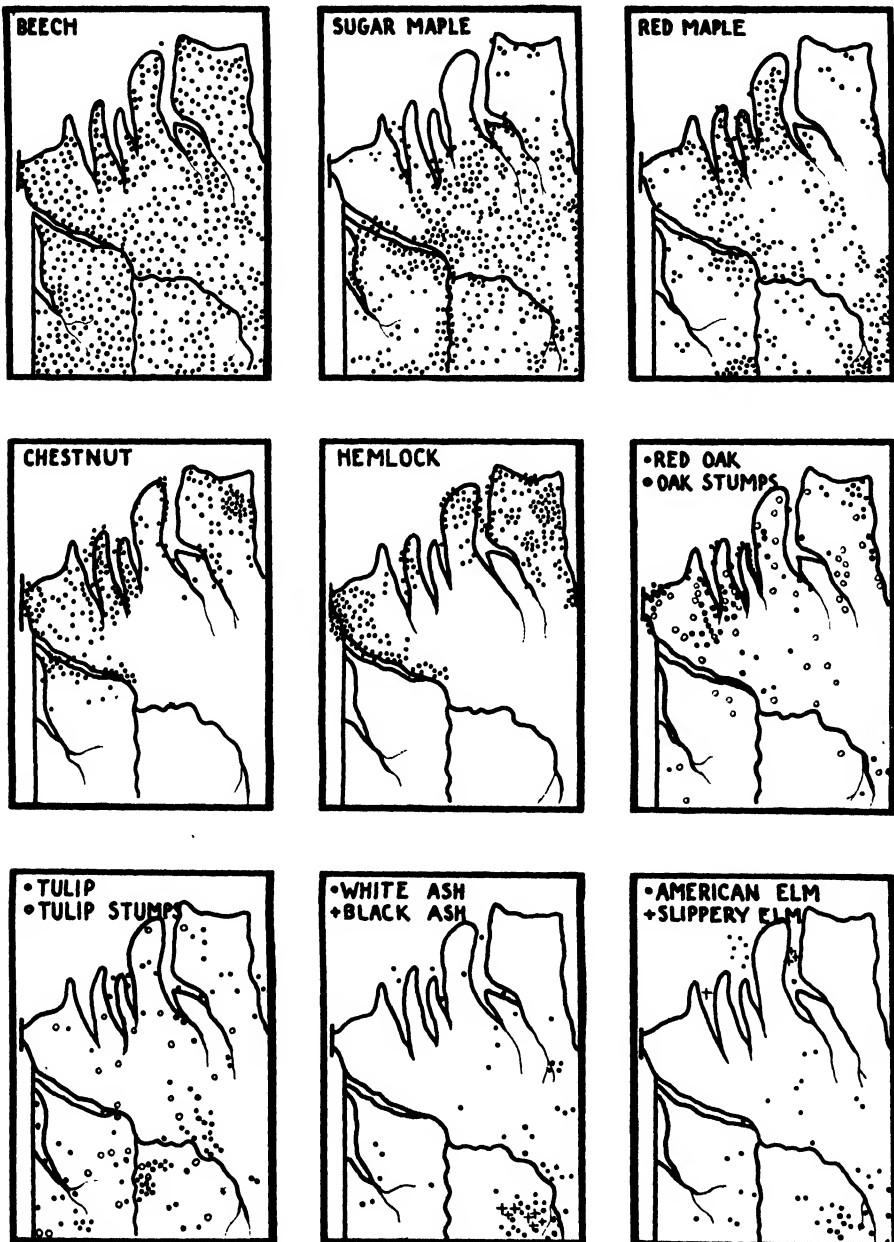
Fig. 9. Distribution of tree species throughout the area under study.

son and grows to larger size than upon the upland. Only here can ferns
be said to be well developed. Trees in the ravines often represent bottom-
land species which have thus extended the flood-plain forest into the area,
bringing in some species which otherwise seem out of place. Beech is
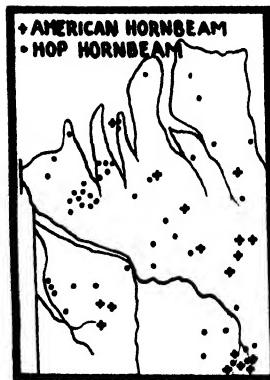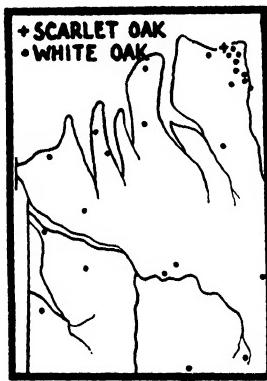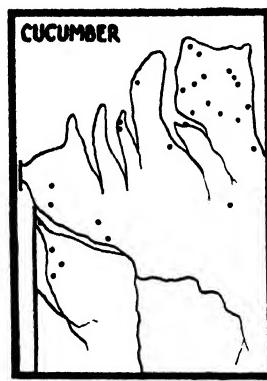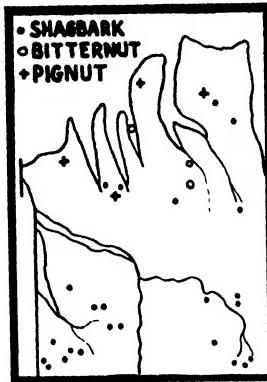
FIG. 10. Distribution of tree species throughout the area under study.

absent from the ravines but sugar maple and tulip are present, and in cer-
tain places hemlock is found in the ravines.   Thus the ravines might be
considered as the beginning of a transition stage toward swamp forest or
flood-plain conditions.

(3) *The western forest edge, and particularly its southwest corner.*
Here, with the exception of some large American elms, the forest is younger
than elsewhere, and its character leads one to believe that a portion of it
may have served at one time as a "wood-lot" in which only the elms were
left undisturbed.   The southwest corner has considerable standing water
in it during most of the year which accounts for the numbers of American
elm, basswood, and red maple here, and the presence of black ash; suggest-
ing the elm-black ash-red maple association described by Sampson (1930)
as characteristic of the swamp forest of northeastern Ohio.

(4) *The interior forest.* This includes the larger part of the area under
study.   The land here is relatively level, and the forest is quite uniformly
beech and sugar maple in varying proportions, including a few other asso-
ciated species as secondary or incidental dominants.

Table 5 shows the abundance and distribution of tree species throughout
the four habitats above described.   Figure 11, following the method used
by Sampson (1930), reduces Table 5 to graphic form.   Scientific names in
this, and in the following lists of vascular plants, are as given in Gray's
Manual of Botany, seventh edition (1908).

Taking the forest as a whole it should be noted that beech composes 51
per cent of it, sugar maple 26.5, red maple 7.2, and hemlock 6.6 per cent.
These four species together thus make up 91.4 per cent of the forest.   In-
asmuch as chestnut has already ceased to be a factor in the community, and,
as will be shown later, hemlock and red oak are tending toward exclusion,
and tulip and white ash are here secondary succession trees, it appears that
the species of greatest importance in this forest are beech, sugar maple,
and red maple.

SUBDOMINANT GREEN PLANTS

In this group belong the shrubs, the herbs, the ferns, the climbers, twiners
and trailers, and other low-growing plants.   As the shrub layer society is
very poorly and irregularly developed throughout the entire area, significant
differences in the distribution of the plants of this list (Table 6) are largely
as between beech-maple and beech-hemlock environments, and their oc-
currence in either or both of these associations is noted.   The order of
listing, except in the case of the uncommon to rare species, or unless other-
wise noted, is in the order of their abundance.

Spicebush is the most abundant shrub in the area, but it is concentrated
largely in two rather moist situations.   Maple-leaved viburnum is better
distributed than spicebush, but occurs only sparingly.   Red-berried elder is

TABLE 5. Species, abundance, and distribution of trees of 3.5 inches in diameter and over.

Species	Beech-maple-association		Beech-hemlock-oak-chestnut mictium		Transition toward swamp forest				Totals	Per cent
					In ravines		Swampy area			
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent		
Beech—*Fagus grandifolia* Ehrh.	1920	52.6	707	43.0	...	....	87	28.4	2714	47.2
Sugar Maple—*Acer saccharum* Marsh.	1193	32.7	124	7.5	19	13.0	79	25.6	1415	24.6
Red Maple—*Acer rubrum* L.	227	6.2	113	7.0	10	7.0	31	10.0	381	6.6
Hemlock—*Tsuga canadensis* (L.) Carr.	36	1.0	242	14.9	72	49.0	....	....	350	6.1
Chestnut—*Castanea dentata* (Marsh.) Borkh.	36	1.0	235	14.9	....	....	....	.....	271	4.7
Tulip—*Liriodendron tulipifera* L.	110	3.0	14	0.9	6	4.0	2	0.7	132	2.3
Red Oak—*Quercus rubra* L.	8	0.2	78	4.8	5	3.4	3	1.0	94	1.6
White Ash—*Fraxinus americana* L.	25	0.7	..	.....	7	4.7	29	9.5	61	1.1
American Elm—*Ulmus americana* L.	18	0.5	...	.....	7	4.7	24	8.0	49	0.9
Hop Hornbeam—*Ostrya virginiana* (Mill.) K. Koch.	18	0.5	21	1.2	....	....	6	2.0	45	0.8
Basswood—*Tilia americana* L.	7	0.2	....	.....	6	4.0	25	8.2	38	0.7
Shagbark Hickory—*Carya ovata* (Mill.) K. Koch.	20	0.5	4	0.2	....	....	7	2.3	31	0.6
Tupelo—*Nyssa sylvatica* Marsh.	5	0.1	21	1.2	....	....	...	.....	26	0.4
Cucumber—*Magnolia acuminata* L.	7	0.2	18	1.1	....	....	.	.....	25	0.4
White Oak—*Quercus alba* L.	7	0.2	16	0.9	...	....	1	0.3	24	0.4
Sassafras—*Sassafras varriifolium* (Salisb.) Ktze.	3	0.1	15	0.9	...	.....	...	. ..	18	0.3
American Hornbeam—*Carpinus caroliniana* Walt.	11	0.3	1	0.0	....	...	6	2.0	18	0.3
Flowering Dogwood—*Cornus florida* L.	1	0.0	10	0.6	....	.....	....	.....	11	0.2
Wild Black Cherry—*Prunus serotina* Ehrh.	1	0.0	5	0.2	3	2.0	....	..	9	0.2
Slippery Elm—*Ulmus fulva* Michx.	...	....	...	.....	6	4.0	..	. ..	6	0.1
Black Ash—*Fraxinus nigra* Marsh.	...	....	...	.....	....	....	6	2.0	6	0.1
Black Walnut—*Juglans nigra* L.	...	..	2	0.1	2	1.4	....	...	4	0.1
Pignut—*Carya glabra* (Mill.) Spach.	...	..	4	0.2	..	.....	...	....	4	0 1
Bitternut—*Carya cordiformis* (Wang.) K. Koch.	1	0.0	...	.....	2	1.4	...	....	3	
Shadbush—*Amelanchier canadensis* (L.) Medic.	....	....	3	0.2	....	.....	....	.....	3	
Butternut—*Juglans cinerea* L.	...	....	...	.....	2	1.4	...	.....	2	} 0.2
Black Birch—*Betula lenta* L.	....	..	2	0.1	....	.....	....	.....	2	
Scarlet Oak—*Quercus coccinea* Muench.	.	.....	1	0.0	....	.....	....	.....	1	
Totals	3654	....	1638	....	147	.....	306	.....	5745	100.0

commonly found as a subseral plant where the soil has been disturbed. In most cases the shrubs give the impression of struggling under severe limitations. Their development is usually poor, and they fruit sparingly except in open situations.

In the beech-maple association the herbaceous plants grow luxuriantly, and produce annually a tremendous crop of seeds, fruits, and other food reserves stored in corms, tubers, root-stocks, and other like structures. Spring beauty, spring cress, cut-leaved dentaria, and yellow adder's tongue occur in great numbers on the higher land where there is usually a surplus of standing water in April and May. In certain places the forest floor may aptly be said to be "carpeted" with the blooms of these species. The two trilliums are very abundant in the mid-portion of the area, and grow to large size in the ravines. Dutchman's breeches is common on the higher ground, while squirrel corn seems to prefer the sides of the ravines. Four

SPECIES	TRANSITION TOWARD SWAMP-FOREST	BEECH-MAPLE ASSOCIATION	BEECH-HEMLOCK-OAK-CHESTNUT MICTIUM
BEECH			
SUGAR MAPLE			
RED MAPLE			
HEMLOCK	(IN RAVINES)		
CHESTNUT			
TULIP			
RED OAK			
WHITE ASH			
AMER. ELM			
H. HORNBEAM			
SHAGBARK			
BASSWOOD			
TUPELO			
CUCUMBER			
WHITE OAK			
SASSAFRAS			
A. HORNBEAM			
F. DOGWOOD			
BLACK CHERRY			
SLIPPERY ELM			
BLACK ASH			
BL. WALNUT			
BUTTERNUT			
BITTERNUT			
PIGNUT			
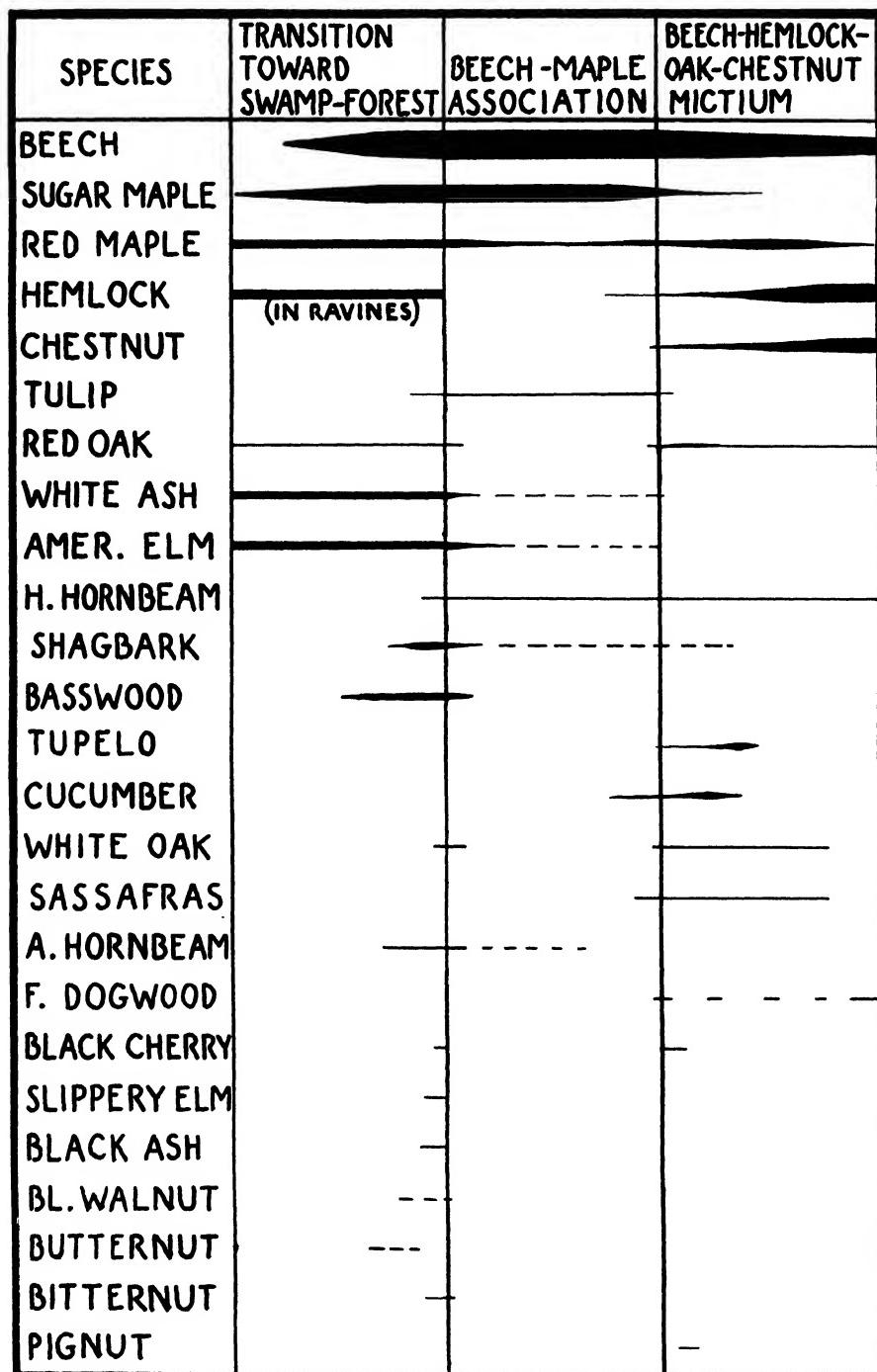
FIG. 11. Distribution and abundance of tree species showing relation to beech-maple association and contiguous forest types.

TABLE 6. Subdominant green plants.

	Beech-maple	Beech-hemlock
1. SHRUBS:		
Spicebush—*Benzoin aestivale* (L.) Nees.	*	
Maple-leaved Viburnum—*Viburnum acerifolium* L.	*	*
Red-berried Elder—*Sambucus racemosa* L.	*	
Highbush Blackberry—*Rubus allegheniensis* Porter.	*	
Prickly Gooseberry—*Ribes cynosbati* L.	*	*
Purple-flowering Raspberry—*Rubus odoratus* L.	*	
Witch Hazel—*Hamamelis virginiana* L.	*	*
Choke Cherry—*Prunus virginiana* L.	*	
Common Elder—*Sambucus canadensis* L.	*	
Fly Honeysuckle—*Lonicera canadensis* Marsh.		*
Bush Honeysuckle—*Diervilla lonicera* Mill.		*
Low Sweet Blueberry—*Vaccinium pennsylvanicum* Lam.		*
Leatherwood—*Dirca palustris* L.		*
2. CLIMBERS, TWINERS, AND TRAILERS:		
Northern Fox Grape—*Vitis labrusca* L.	*	
Trailing Euonymus—*Evonymus obovatus* Nutt.	*	*
Virginia Creeper—*Psedera quinquefolia* (L.) Greene	*	
Poison Ivy—*Rhus toxicodendron* L.	*	
Green Brier—*Smilax rotundifolia* L.	*	
Carrion Flower—*Smilax herbacea* L.	*	
Bittersweet—*Celastrus scandens* L.	*	
3. HERBS AND LOW SHRUBBY PLANTS:		
a. Abundant species (somewhat in the order of their flowering)		
Hepatica—*Hepatica acutiloba* DC.	*	
Spring Beauty—*Claytonia virginica* L.	*	
Yellow Adder's Tongue—*Erythronium americanum* Ker.	*	
Round-leaved Violet—*Viola rotundifolia* Michx.	*	
Halberd-leaved Violet—*Viola hastata* Michx.	*	
Wake Robin—*Trillium erectum* L.	*	
Dutchman's Breeches—*Dicentra cucullaria* (L.) Bernh.	*	
Cut-leaved Dentaria—*Dentaria laciniata* Muhl.	*	
Spring Cross—*Cardamine bulbosa* (Schreb.) BSP.	*	
Squirrel Corn—*Dicentra canadensis* (Goldie) Walp.	*	
Rue Anemone—*Anemonella thalictroides* (L.) Spach.	*	
Great White Trillium—*Trillium grandiflorum* (Michx.) Salisb.	*	
Wild Ginger—*Asarum canadense* L.	*	
Sweet Cicely—*Osmorhiza claytoni* (Michx.) Clarke	*	
Toothwort—*Dentaria diphylla* Michx.	*	
Oakesia—*Oakesia sessilifolia* (L.) Wats.	*	
Downy Yellow Violet—*Viola pubescens* Ait.	*	
Smooth Yellow Violet—*Viola scabriuscula* Schwein.	*	
Canada Violet—*Viola canadensis* L.	*	
Dwarf Ginseng—*Panax trifolium* L.	*	
Foam Flower—*Tiarella cordifolia* L.	*	
Solomon's Seal—*Polygonatum biflorum* (Walt.) Fll.	*	
Canada Mayflower—*Maianthemum canadense* Desf.		*
Jack-in-the-Pulpit—*Arisaema triphyllum* (L.) Schott.	*	
May Apple—*Podophyllum peltatum* L.	*	
False Spikenard—*Smilicina racemosa* (L.) Desf.	*	
Pale Jewelweed—*Impatiens pallida* Nutt.	*	
Spotted Jewelweed—*Impatiens biflora* Walt.	*	
Pokeweed—*Phytolacca decandra* L.	*	
b. COMMON SPECIES:		
Blue Cohosh—*Caulophyllum thalictroides* (L.) Michx.	*	
Large-flowered Bellwort—*Uvularia grandiflora* Sm.	*	
Swamp Buttercup—*Ranunculus septentrionalis* Poir.	*	

TABLE 6. Continued

	Beech-maple	Beech-hemlock
Yellow Rocket—*Barbarea vulgaris* R. Br.	*	
Common Violet—*Viola papilionacea* Pursh	*	
Indian Cucumber—*Medeola virginiana* L.	*	*
Wild Sarsaparilla—*Aralia nudicaulis* L.	*	
Twisted Stalk—*Streptopus amplexifolius* (L.) DC	*	
Partridgeberry—*Mitchella repens* L.		*
White Baneberry—*Actaea alba* (L.) Mill.	*	
Wild Blue Phlox—*Phlox divaricata* L.	*	
Wild Geranium—*Geranium maculatum* L.	*	
Northern Bedstraw—*Galium boreale* L.	*	
Black Snakeroot—*Cimicifuga racemosa* (L.) Nutt.	*	
Wintergreen—*Gaultheria procumbens* L.		*
Richweed—*Pilea pumila* (L.) Gray	*	
c. UNCOMMON TO RARE SPECIES:		
Harbinger of Spring—*Erigenia bulbosa* (Michx.) Nutt.	*	
Bloodroot—*Sanguinaria canadensis* L.	*	
Trailing Arbutus—*Epigaea repens* L.		*
Perfoliate Bellwort—*Uvularia perfoliata* L.	*	
Early Meadow Rue—*Thalictrum dioicum* L.	*	
Wood Anemone—*Anemone quinquefolia* L.	*	
Wood Betony—*Pedicularis canadensis* L.	*	
Sweet White Violet—*Viola blanda* Willd.	*	
Great-spurred Violet—*Viola rostrata* Pursh.	*	
Wood Sorrel—*Oxalis corniculata* L.	*	
Bishop's Cap—*Mitella diphylla* L.	*	
Golden Seal—*Hydrastis canadensis* L.	*	
Virginia Waterleaf—*Hydrophyllum virginianum* L.	*	
Pink Lady's Slipper—*Cypropedium acaule* Ait.		*
Agrimony—*Agrimoria striata* Michx.	*	
Monkey Flower—*Mimulus ringens* L.	*	
Round-leaved Orchid—*Habenaria orbiculata* (Pursh.)	*	
Great Lobelia—*Lobelia siphilitica* L.	*	
Wild Leek—*Allium tricoccum* Ait.	*	
Ginseng—*Panax quinquefolium* L.	*	
Indian Tobacco—*Lobelia inflata* L.	*	
Cardinal Flower—*Lobelia cardinalis* L.	*	
Nodding Pogonia—*Pogonia trianthophora* (Sw.) BSP	*	
Spikenard—*Aralia racemosa* L.	*	
4. FERNS:		
Christmas Fern—*Polystichum acrostichoides* (Michx.) Schot.	*	*
Spinulose Wood Fern—*Asplenium spinulosum intermedium* D. C. Eaton	*	*
Silvery Spleenwort—*Asplenium acrostichoides* Sw.	*	*
New York Fern—*Aspidium noveboracense* (L.) Sw.	*	*
Marginal Shield Fern—*Aspidium marginale* (L.) Sw.	*	*
Rattlesnake Fern—*Botrychium virginianum* (L.) Sw.	*	
Broad Beech Fern—*Phegopteris haxagonoptera* (Michx) Fee.	*	*
Maidenhair Fern—*Adiantum pedatum* L.	*	
Long Beech Fern—*Phegopteris polypodioides* Fee.	*	
Sensitive Fern—*Onoclea sensibilis* L.	*	
Ternate Grape Fern—*Botrychium ternatum intermedium* D. C. Eaton	*	
Interrupted Fern—*Osmunda claytoniana* L.	*	
Narrow-leaved Spleenwort—*Asplenium angustifolium* Michx.	*	(in ravines)
Hay-scented Fern—*Dicksonia punctilobula* (Michx.) Gray	*	

TABLE 6. Continued

	Beech-maple	Beech-hemlock
5. MOSSES:		
Amblystegium serpens (L.) B & S.	*	*
Thuidium delicatulum (L.) Mitt.	*	
Hypnum haldanianum Grev.	*	
Hypnum reptile Mx.	*	
Funaria hygrometricia (L.) Sibth.	*	
Leucobryum glaucum (L.) Schimp.		*
Mnium cuspidatum (L.) Leyss.	*	*
Dicranella heteronalla (L.) Schimp.	*	*
Catharinea undulata (L.) W & M.	*	
Fissidens taxifolius (L.) Hedw.	*	
6. MISCELLANEOUS:		
Sedge—*Carex plantaginea* Lam.	*	
Club Moss—*Lycopodium lucidulum* Michx.		*
Lichen—*Cladonia fimbriata* (L.) Hoffm. Deutsch.	*	*
Liverwort—*Marchantia polymorpha* (L.).	*	
Alga—*Microspora amoena* (Kütz.) Lagerh.	*	
Alga—*Protococcus* sp. (on beech trunks)	*	*

species of yellow violets bloom abundantly. Hepatica grows in masses in moist places along the water-courses and on the edges of the ravines. False spikenard, solomon's seal, and twisted stalk are quite generally distributed. Wild ginger and May apple cover the ground with their characteristic leaves in certain locations. Jack-in-the-pulpit and blue cohosh are well distributed. The tiny dwarf ginseng, in its season, shows its small puff-balls of white bloom throughout the forest. The evergreen leaves of foam flower are common in the wetter places, and over the edges of the ravines. Those curious plants, beech drops, and squaw root, are common, the former more so than the latter; and the pale Indian pipe is found frequently. The late-comers, white baneberry and black snake-root, are common. Jewelweed and pokeweed grow luxuriantly in certain places.

In great contrast to this rich development of herbaceous growth beneath the beeches and maples is the thinly spread ground cover beneath the hemlocks. The common herbaceous plant of the beech-hemlock association is the Canada mayflower. In certain locations it covers the ground, but it is the only plant of which this can be said. In this environment partridge berry and wintergreen appear frequently. Apart from these there is very little. It is in this habitat that a few plants of pink lady's slipper and trailing arbutus occur.

This difference in herbaceous growth was studied in Indiana by Daubenmire (1930), who concluded that, of the factors studied (light, evaporation rate, soil acidity, soil moisture), soil moisture conditions exerted the most inhibitive influence on vegetational development under hemlock, while the

greater acidity of the surface soil is probably a contributing factor in the inhibition of forest floor herbs.

In no place in the area do ferns grow in abundance. Small societies of New York fern occur sparingly on the higher land and on some of the spurs. Christmas fern, marginal shield fern, and spinulose wood fern are all well distributed as individual plants, reaching their best development along the edges of the gullies and ravines. Rattlesnake fern is well distributed on the higher land. Other ferns on the list occur only occasionally. In general, while most of these ferns may be found in both associations, they are more abundant in beech-maple than in beech-hemlock environment, and are best developed in the ravines and along their sides. There is little poison ivy in the area, and such as there is, is confined to the beech-maple association on higher ground. In places Virginia creeper grows as ground cover, and in a few places it ascends the trees. In certain locations in the beech-maple association trailing euonymus forms dense mats as ground cover.

The vine *par excellence* in the area is the northern fox grape. It may form tangles in the tops of large standing trees, or hang in a dense "curtain" from lofty supports, or create tangles on the ground when the original supporting trees have broken down, letting the whole mass down to ground level. In the latter case a great opening is made in the forest canopy. Secondary succession after grapes is obscure, as nothing grows beneath the grapes in this condition.

Neither mosses nor lichens are particularly abundant in the area. Probably the creeping hypnum, *Amblystegium serpens*, growing on logs and stones, is the most common moss in the beech-maple association, and the cushion moss, *Leucobryum glaucum*, is the most common in the beech-hemlock association. The sedge, *Carex plantaginea*, is one of the well distributed plants of the beech-maple association.

SAPROPHYTES AND PARASITES

Saprophytic and parasitic plants in the area fall in two main groups—flowering plants and fungi. They are listed in Table 7. Although the fungi listed represent four seasons of observation it is realized that the list is far from complete, as new species are constantly being added. However, it may be assumed that those species that are of greatest importance in the area, because of their abundance, regularity of appearance, or wide distribution, are noted herein.

Doubtless because of the long time during which the natural processes of decay have been at work in the forest under study, the number of species, and the abundance of certain fungi, is great. In fact, Mr. Henry C. Beardslee, an authority on Ohio fungi, gives it as his opinion that from 1,200 to

TABLE 7. Saprophytic and parasitic plants.

1. Flowering plants.
   Beech Drops—*Epifagus virginiana* (L.) Bart.   (beech-maple association)
   Squaw Root—*Conopholis americana* (I.f.) Wallr.   (beech-hemlock association)
   Indian Pipe—*Monotropa uniflora* L.   (beech-maple association)
2. Fungi.
   A. Abundant fungi (in order of abundance)
      a. Woody brackets
         Polyporus applanatus Fr.
         Polyporus resinosus (Fr.) Schrader.
         Polyporus gilvus (Fr.) Schw.
      b. Leathery brackets
         Polyporus versicolor Fr.
         Polystictus pergamenus Fr.
         Stereum spadiceum Fr.
         Polyporus hirsutus Schw.
      c. Gilled mushrooms
         Collybia radicata Rehl.
         Armillaria mellea Vahl.
         Pleurotus ostreatus Jacq.
         Hypholoma sublateritium Schaeff.
         Hypholoma perplexum Pk.
         Clitopilus abortivus B & C.
         Mycena Leajana Berk.
         Coprinus atramentarius (Bull.) Fr.
         Collybia platyphylla Fr.
      d. Puff-balls
         Lycoperdon pyroforme Schaeff.
         Scleroderma aurantium (Vaill.) Pers.
      e. Gelatinous fungi
         Tremella mesenterica Retz.
         Exidia glandulosa (Bull.) Fr.
      f. Chestnut blight
         Endothia parasitica (Murr.) Ander. and Ander.
   B. Common fungi (not in order of abundance)
      a. Woody and leathery polypores
         Polyporus lucidus (Leys.) Fr.
         Polyporus sulphureus (Bull.) Fr.
         Fomes fomentarius Fr.
         Polyporus brumalis (Pers.) Fr.
      b. Gilled mushrooms
         Amanita verna Fr.
         Amanitopsis vaginata Roze.
         Claudopus nidulans (Pers.) Pk.
         Clitocybe illudens Schw.
         Clitocybe infundibuliformis Schaeff.
         Collybia velutipes Curt.
         Collybia strictipes Pk.
         Coprinus micaceous (Bull.) Fr.
         Crepidotus versutus Pk.
         Gomphidius rhodoxanthus Schw.
         Hypholoma appendiculatum Bull.
         Lepiota procera Scop.
         Marasmius rotula Fr.
         Marasmius siccus (Schw.) Fr.
         Mycena haemptopoda Pers.
         Mycena galericulata Scop.
         Omphalia campanella Batsch.
         Pholiota adiposa Fr.
         Pleurotus sapidus Kalchb.
         Pleurotus serotinoides Fr.

         Pluteus cervinus Schaeff.
         Russula emetica Fr.
         Russula fragilis Fr.
         Russula mariae Pk.
         Strobilomyces strobilaceus Berk.
    c. Boletaceae
         Boletus felleus Bull.
         Boletus edulis Bull.
         Boletus peckii Frost.
         Boletinus porosus (Berk.) Pk.
         Fistulina hepatica Fr.
    d. Puff-balls
         Geaster triplex Jungh.
         Lycoperdon gemmatum Batsch.
    e. Coral fungi
         Clavaria flava Schaeff.
         Clavaria cinerea Bull.
    f. Spore-sac fungi (Ascomycetes)
         Peziza coccinea Jacq.

  C. Uncommon to rare fungi (not in order of abundance)
    a. Gilled mushrooms

Agaricus sylvaticus Schaeff.	*Agaricus sylvicola* Vitt.
Amanita flavorubescens Atk.	*Amanita muscaria* L.
Amanita rubescens Fr.	*Amanita solitaria* Bull.
Armillaria amianthina Fr.	*Cantherellus aurantiacus* Fr.
Cantherellus cibarius Fr.	*Cantherellus rosellus* Pk.
Cantherellus umbonatus Fr.	*Clitocybe adirondackensis* Pk.
Clitocybe albissima Pk.	*Clitocybe candida* Bres.
Clitocybe clavipes Pers.	*Clitocybe cyathiforme* Fr.
Clitocybe fragrans Sow.	*Clitocybe laccata* Scop.
Clitocybe multiceps Pk.	*Clitocybe multiformis* Pk.
Clitocybe nebularis Batsch.	*Clitocybe ochropurpurea* Berk.
Clitocybe odora Bull.	*Clitocybe picceina* Pk.
Clitocybe subcyathiforme Pk.	*Clitopolis noveboracense* Pk.
Clitopolis orchella Fr.	*Collybia butyracea* Fr.
Collybia confluens Pers.	*Collybia colorea* Pk.
Collybia dryophila Fr.	*Collybia tuberosa* Fr.
Coprinus comatus Fr.	*Cortinarius alboviolaceus* Fr.
Cortinarius distans Pk.	*Cortinarius duracinus* Fr.
Crepidotus applanatus Fr.	*Crepidotus fulvotomentosus* Pk.
Crepidotus malachius B & C.	*Darcomyces deliquescens* (Bull.) Duby.
Entoloma jubatum Pk.	*Entoloma niderosum* Fr.
Entoloma rhodopolium Fr.	*Entoloma strictus* Pk.
Flammula flavida Fr.	*Flammula lenta* Fr.
Flammula spumosa Fr.	*Hygrophorus cantherellus* Schw.
Hygrophorus ceraceus Fr.	*Hygrophorus chlorophanus* Fr.
Hygrophorus fulgineus Frost.	*Hygrophorus miniatus* Fr.
Hygrophorus pratensis Fr.	*Hygrophorus coccineus* Schaeff.
Hygrophorus conicus Fr.	*Hypholoma echinoceps* Atk.
Hypholoma hydrophilum Fr.	*Hypholoma lachrymabundum* Fr.
Hypholoma rugocephalium Atk.	*Inocybe radiata* Pk.
Lactarius chrysorheus Fr.	*Lactarius cinereus* Pk.
Lactarius fuliginosus Fr.	*Lactarius helvus* Fr.
Lactarius hysginus Fr.	*Lactarius piperatus* Scop.
Lactarius subdulcis Fr.	*Lactarius trivialis* Fr.
Lactarius vietus Fr.	*Lactarius volemus* Fr.
Lentinus ursinus Fr.	*Lenzites betulina* Fr.
Lepiota acutaesquamosa Fr.	*Lepiota clypeolaria* Fr.
Lepiota cristata Fr.	*Lepiota metulaespora* B & Br.
Lepiota naucina Fr.	*Leptonia asprella* Fr.
Leptonia formosa Fr.	*Marasmius delectans* Morg.

Marasmius elongatipes Pk.
Marasmius creades Fr.
Marasmius spongiosus B & C.
Marasmius velutipes B & C.
Mycena albolutea Pk.
Mycena alkalina Fr.
Mycena cohaerens Fr.
Mycena filopes Fr.
Mycena minutula Pk.
Mycena peliantha Fr.
Mycena polygramma Bull.
Mycena pulcherrima Pk.
Mycena pura Fr.
Nectria cinnibarina (Tode.) Fr.
Nolanea pascua Fr.
Omphalia fibula Fr.
Panus strigosus B & C.
Panus rudis Fr.
Panus stypticus Fr.
Panus torulosis Fr.
Paxillus lepista Fr.
Paxillus panucides Fr.
Pholiota erebia Fr.
Pholiota marginata Batsch.
Pholiota mutabilia Fr.
Pholiota praecox Pers.
Pholiota spectabilis Fr.
Pholiota squarrosa Müll.
Pholiota squarrosoides Pk.
Pleurotus corticatus Fr.
Pleurotus petaloides Bull.
Pleurotus ulmarius Fr.
Pluteolus reticulatus Fr.
Pluteus admirabilis Pk.
Pluteus granularis Pk.
Pluteus longistriatus Pk.
Russula alutacea Fr.
Russula foetans Fr.
Russula lepida Fr.
Russula lutea (Huds.) Fr.
Russula pusilla Pk.
Russula purpurina Quel. & Sch.
Russula sordida Pk.
Russula rubescens Beards.
Russula uncialis Pk.
Russula sanguinea Fr.
Russula vinosa Lindb.
Stropharia squamosa (Pers.) Fr.
Tricholoma laterarium Pk.
Tricholoma personatum Fr.
Volvaria bombycina Schaeff.

b. Boleti

Boletus alutaceus Morg.
Boletus castaneus Bull.
Boletus chrysenteron Fr.
Boletus diochrous Ellis.
Boletus scaber Fr.
Boletus subtomentosus Fr.

c. Puff-balls

Calvatia cyathiformis Bosc.
Geaster hygrometricus Pers.
Lycoperdon echinatum Pers.
Lycoperdon subincarnatum Pk.
Cyathus striatus Willd.

d. Spore-sac fungi (Ascomycetes)

Bulgaria inquinans Fr.
Geoglossum
Gyromitra esculenta Fr.
Helvella crispa Fr.
Morchella esculenta Pers.
Peziza aurantia Pers.
Peziza badia Pers.
Peziza odorata Pk.
Peziza scutellata
Xylaria polymorpha Pers.

e. Polypores

Daedalia ambigua Berk.
Daedalia confragosa Boton.
Favolus canadensis Klotsch.
Merulius lachrymans (Jacq.) Fr.
Polyporus cinnibarinus Jacq.
Polyporus frondosus Fr.
Polyporus galactinus Berk.
Polyporus picipes Fr.
Polyporus radicatus Schw.
Polyporus squamosus Fr.
Polyporus umbellatus Fr.

f. Other species

Clavaria amethystina Bull.
Clavaria aurea Schaeff.
Clavaria inequalis Fl. Dan.
Clavaria mucida Pers.
Clavaria muscoides Fr.
Clavaria vermicularis Scop.
Hydnum caput-ursi Fr.
Hydnum coralloides Scop.
Hydnum erinaceus Bull.
Hydnum repandum (L.) Fr.
Hydnum septentrionale Fr.
Tremella albida Huds.
Tremella lutescens Pers.
Tremellodon gelatinosum Pers.
Tremalitelia nucleata (Seb.) Rea.
Hyroneola auricula-judae (L.) Berk.
Craterellus cantherellus Schw.
Stereum sericium Schw.
Phallus ravenelii B & C.
Mutinus elegans (Mont.) Ed. Fischer.

1,500 species of the larger fungi should eventually be listed in such a forest as this. Of the woody sporophores that are persistent as brackets throughout the year, those of *Polyporus applanatus* are by far the most abundant. Usually these are the first of the brackets to appear upon newly fallen tree trunks, and often appear upon living trees. Even in such a case, however, they are probably growing on dead wood (Von Schrenk and Spaulding 1909). This fungus has been noted upon the decaying logs of practically all of the species of trees within the area.

Of the leathery polypores, *Polyporus versicolor* is in evidence everywhere, and usually its banded ruffles are the first fungus growth to appear upon fallen logs or branches of whatever species. *Stereum spadiceum* and *Polystictus pergamenus* may frequently be found in close competition with *Polyporus versicolor*. The service of these fungi and a few other closely related species in the forest under study in helping return to the soil the mass of woody plant débris which otherwise would continually accumulate can scarcely be overestimated. Bray (1915) points out that if it were not for some such disintegrating force at work in the forest, the surface of the ground would soon become clogged to such an extent as to make further plant growth impossible. Considering the number of species of fungi recorded at North Chagrin, and the great abundance of their sporophores at certain seasons, it is apparent that the humus must be thoroughly permeated with fungus mycelium, and that the fallen leaves, branches, and tree trunks are all "hot beds" of fungus activity.

The presence and the fruiting bodies of slime moulds (Myxomycetes) have been frequently noted, but no attempt has as yet been made to study their distribution or significance.

DYNAMICS OF SUCCESSION

Throughout the area the presence of old stumps, logs, and standing dead trees indicates something of the character of the forest of the recent past. Despite the passage of more than 60 years it is possible to recognize three species of trees represented by the stumps said to have been cut in 1871. These are oak (probably red oak, as this is the present most abundant species of oak), tulip, and chestnut. The species maps of tulip and red oak (Fig. 10) show both the living trees and the old stumps. It is apparent that red oak was formerly a constituent of the interior forest in much greater numbers than now. The 50 oak stumps that were measured showed an average diameter, without bark of sapwood, of 38.2 inches (97.03 cm.) at approximately 3 feet (91.44 cm.) from the ground. The average diameter of the 50 largest living red oaks is 30.2 inches (76.7 cm.) Apparently the stumps represent a considerably more mature stand than do the present trees.

There are 32 stumps of tulip recognizable at the present time. Measurements of these show an average diameter of 32.8 inches (83.31 cm.) without bark, at approximately 3 feet from the ground. The largest 32 living tulips show an average diameter of 29.6 inches (75.18 cm.), a size not greatly below that of the old stumps. A study of the species map (Fig. 10) indicates that the position of tulip in the community has changed little, if any, in the past 60 years.

The chestnut stumps cut in other years are few in number and are all located in present chestnut territory, indicating no recent movement of chestnut.

On the forest floor it is possible to recognize logs of beech, sugar maple, sassafras, tulip, tupelo,[2] cucumber, and hemlock. Of these, sassafras, cucumber, and hemlock are the only species that, from the position of the logs in the area, indicate a change in distribution as compared with the present. Of the standing dead trees, only cucumber and hemlock exhibit change of distribution. Sassafras and cucumber are apparently in process of being eliminated from the interior forest, as both formerly occurred there but are now practically limited to the spurs or their immediate vicinity (Fig. 10). Hemlock appears to be rapidly decreasing in numbers. Figure 12 shows the location of 85 standing dead hemlocks measuring from 10 inches (25.4 cm.) to 28.6 inches (73.2 cm.) in diameter. The discovery of the larvae of the flat-headed hemlock borer (*Melanophila fulvoguttata* Harr.) beneath the bark of many trees leads to the supposition that the activities of this insect is the immediate cause of the death of these otherwise apparently sound hemlocks. A comparison of Figure 12 with Figure 9 will show that these trees are in the heart of the present hemlock areas.

The rate of reproduction may have a large bearing upon the matter of stability or change in status of the forest constituents. The seeding of both beech and sugar maple is periodically abundant, but beech seedlings do not survive as well as those of sugar maple in the early stages of their development. In one area of approximately 25 feet (7.62 m.) square, 12 beech trees of from 2 to 4 seasons growth were counted, while the number of sugar maples of the same age in the same area was estimated to be in the neighborhood of 3,000—a proportion of 1 beech to 250 sugar maples. Yet the high mortality of young sugar maple saplings later seems to more than make up for this great difference in the early years of development. At present the seeding of both of these trees seems to be adequate to the needs of replacement of the species to make good the annual losses from the ranks of the old trees, and beech has the additional advantage of sending up suckers from the roots.

[2] Wherever "tupelo" is used in this paper the author refers to the common black gum, *Nyssa sylvatica* Marsh., and not *Nyssa aquatica* Marsh. which is most commonly called "tupelo" throughout the Southeast.—Ed.

LOCATION OF BELT TRANSECT
LOCATION OF 85 STANDING
DEAD HEMLOCKS 9.5
TO 22.2 IN. (24.13 TO
56.3 CM.) IN DIAMETER
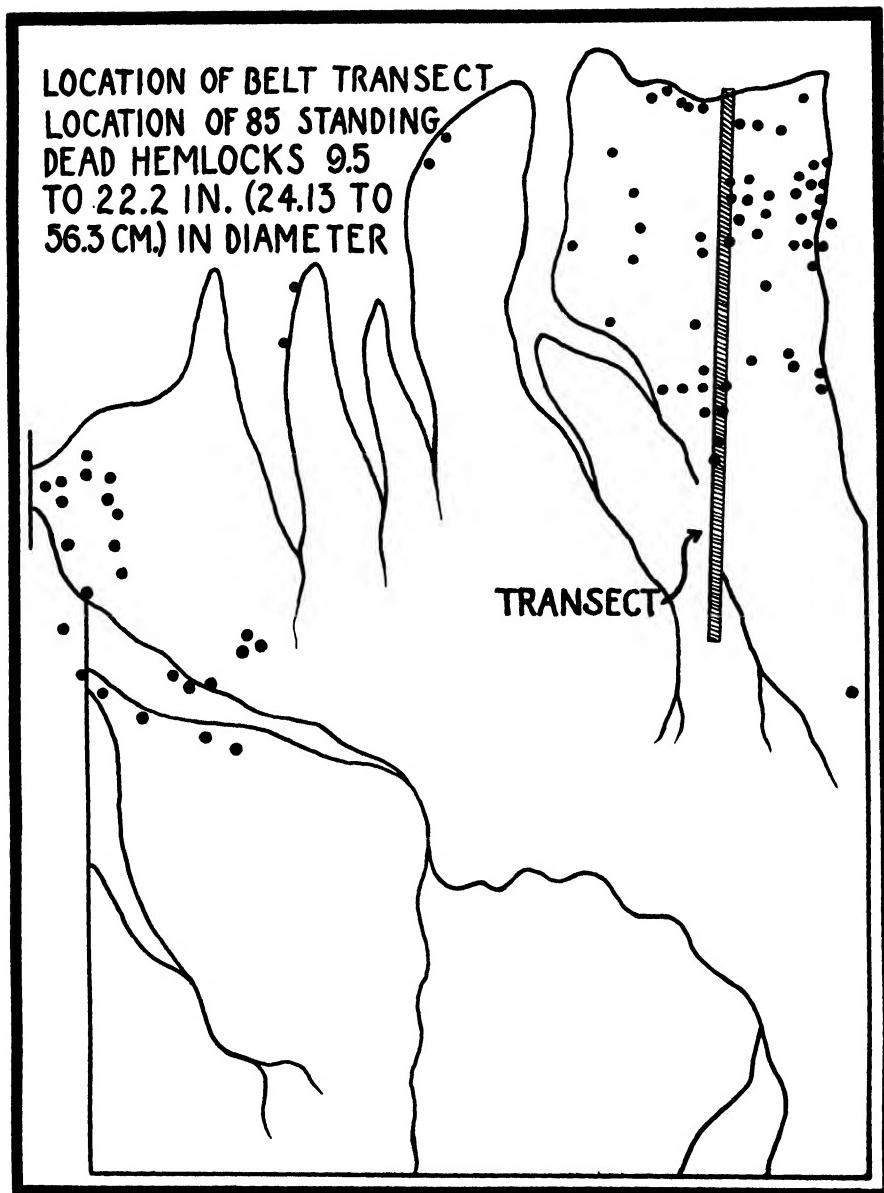
TRANSECT

Fig. 12. Location of standing dead hemlocks. Location of belt transect.

According to Illick and Frantz (1928) under favorable conditions in Pennsylvania dense stands of beech will develop from root suckers alone.

While the seeding of red maple is at times very abundant, germination is poor, and seedlings and saplings do not survive in competition with those of beech and sugar maple.

The hemlocks of the area at times bear abundant crops of seeds, but germination has long been practically at a standstill. Apparently because of more favorable moisture conditions there was a fair amount of germination of hemlock seeds in 1935, but it remains to be seen whether or not a succeeding dry summer may wipe them out. In the hemlock areas it is quite noticeable that the dead leaves of beech and maple make up the bulk of the litter under the trees.

Both tulip and white ash bear seeds regularly and abundantly, and their seeds germinate well, but neither species long survives in competition with seedlings of beech and sugar maple. It is only in those places where sunlight has been let in, usually because of the fall of a large tree, that ash and tulip are able to raise their heads and make a place for themselves in the forest community. Under such conditions they make rapid growth.

Red oak and white oak often bear large quantities of acorns. Red oak in particular often so covers the ground with its seeds that they blanket everything else. Yet there are practically no oak seedlings or saplings of any kind in the forest.

The few hickories in the area produce good crops of nuts, yet there are no seedling or sapling hickories to be found away from the forest edge.

Cucumber and tupelo are regular seeders, and a considerable number of very young trees of these species are to be found in the neighborhood of the old trees. In addition, both of these species will sucker from exposed roots or the bases of stumps.

In order to study more definitely the relative significance of beech, sugar maple, and hemlock in the climax community, a belt transect was charted from a point in the beech-maple association on the higher ground, almost directly east to the edge of the bluff, thus traversing the entire width of the most extensive beech-hemlock territory in the area. Reference to Figure 12 will show its location.

The belt was 10 meters (32.8 feet) in width, and extended for a total distance of 360 meters (1181.1 feet). It was subdivided into 45 quadrats, each 10 by 8 meters (32.8 by 26.2 feet). The approximate position of all trees 2.5 cm (1 inch) or over in circumference was charted in each of these quadrats, and the trees measured breast high by tape. This chart is shown in Figure 13. A study of it reveals the following facts:

1. Beech is represented by large trees throughout the transect—32 of these ranging from 24 cm. (9.4 inches) to 80 cm. (31.5 inches) in diameter.

2. Sugar maple decreases in size as the hemlock area is approached, until it is represented only by saplings, and then soon drops out altogether.

3. Many decaying logs of hemlock on the ground are encountered before the present beech-hemlock association is reached. This condition persists well
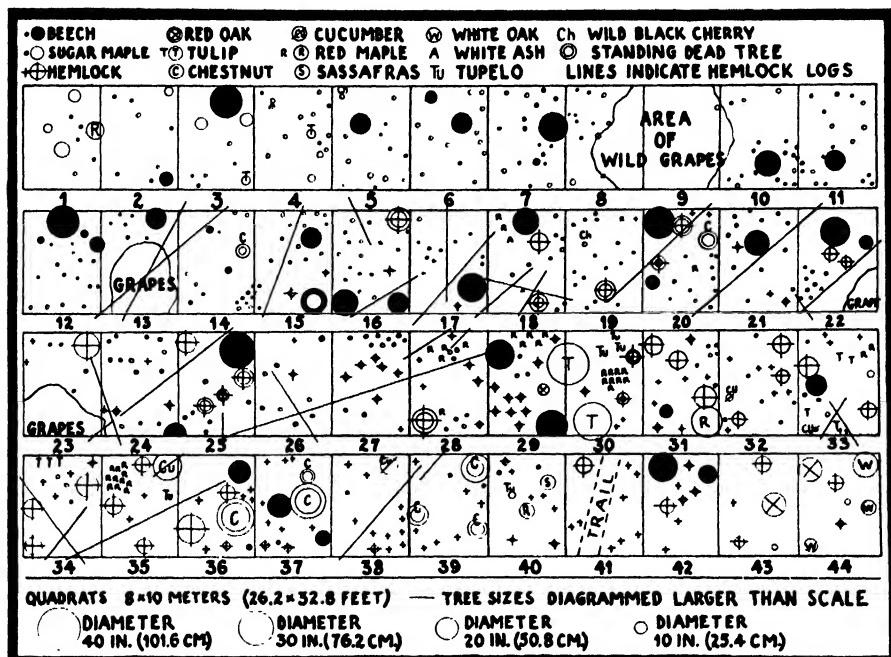
FIG. 13.   Belt transect.

into the present beech-hemlock territory, but becomes less marked as the best hemlock development is reached.   Practically all down timber in the transect is hemlock.

4.   Reproduction of both beech and sugar maple, as represented by saplings and young growth in the transect is good.   Reproduction of hemlock is poor—almost negligible.

5.   The presence of large tulip, tupelo, cucumber, and chestnut is noted—the tulip outside the beech-hemlock territory, the other species associated with the hemlocks.   The presence of oaks is noted as the edge of the bluff is reached.

6.   Red maple appears as a rather constant but not important element in the transect.

A consideration of the age of the community under study may shed some additional light on the dynamics of succession.   Table 8 shows the distribution of the most important tree species through certain size classes.   It will be noted that all of the species here shown exhibit a peak of numbers in what might be called the middle size classes, with diminishing numbers toward both larger and smaller sizes.   Although not shown in this table it is a fact that both beech and sugar maple show much larger numbers in smaller sizes than those included in Table 8.   This is shown by the counts

recorded in Table 5, as well as by general observation. Sugar maple especially, in certain locations, has produced a tremendous number of saplings of from an inch to three inches in diameter. These dense stands of young maples are not of general distribution. They probably represent the heavy seeding of certain old trees under especially favorable circumstances in former years. Mortality among such young trees must be very great when a certain critical point in their development is reached, as Mr. Percy Parker, who has lived many years in the neighborhood, tells the writer that certain areas that are now practically clear of understory trees used to be densely crowded with sugar maple saplings when he used to hunt rabbits in these woods as a boy. In this connection it is interesting to note that one of the very areas thus pointed out by Mr. Parker and now devoid of young saplings, was recently covered (1935) with hundreds of thousands of sugar maple seedlings, standing so closely together as to provide a ground cover of continuous green throughout the summer, where in the previous years of this study the aspect had invariably been that of the almost unbroken brown of dead leaves.

It is of interest to note (Table 8) the decrease in numbers of individuals as the older trees (larger sizes) are considered. They seem to be approaching a limit of size that is rather definitely set.

TABLE 8. Numbers of trees in different size classes.

	DIAMETERS							
Inches.........	9.5 - 12	12 - 15	15 - 18	18 - 21	21 - 24	24 - 27	27 - 30	30 - 33
Centimeters.....	24.1 - 30.4	30.4 - 38.1	38.1 - 45.7	45.7 - 53.3	53.3 - 60.9	60.9 - 68.5	68.5 - 76.2	76.2 - 83.8
Beech............	17	71	132	112	162	81	63	10
Sugar Maple.......	127	173	105	78	61	31	10	2
Red Maple........	56	93	83	48	29	9	4	3
Hemlock..........	79	103	73	39	26	2	2	0
Chestnut..........	13	38	44	55	48	19	24	15
Tulip.............	29	19	4	1	6	5	4	5
White Ash.........	10	12	14	4	3	6	3	1
Red Oak..........	5	7	9	14	12	20	10	10

	DIAMETERS							
Inches.........	33-36	36 - 39	39 - 42	42- 45	45 - 48	48 - 51	......	63.2
Centimeters....	83.8-91.4	91.4 - 99.0	99.0-106.6	106.6 - 114.3	114.3 - 121.9	121.9 - 129.5	......	160.5
Beech............	9	4	3	1	..	..	..	..
Sugar Maple.......	1	1	0	1	..	..	..	..
Red Maple........	3	2	1	1	..	..	..	..
Hemlock..........	0	0	0	0	..	..	..	..
Chestnut..........	6	3	2	2	..	..	..	..
Tulip.............	4	3	2	1	..	..	..	..
White Ash.........	2	0	0	0	..	..	..	..
Red Oak..........	3	0	2	0	1	1	.	1

To this the red oak seems to be the only exception, although it is probable that if it were not for the cutting of some large tulips in 1871 tulip would appear in sizes beyond those of the present table.

It has been possible to make counts of annual rings in a few cases of trees overturned in the area by a severe wind storm June 26, 1931. These records are shown in Table 9. In estimating the age of such a tree, a considerable period of time must be allowed for early stages of growth, as such trees growing from the forest floor, are greatly repressed during the early years.

TABLE 9. Counts of annual rings of trees overturned by storms.

BEECH			
Diameter at cut	Distance from cut to base of tree	Annual rings at cut	Estimated age of tree in years
22 in. (55.8 cm.)	43 in. (1.09 m.)	229	250
20 in. (50.8 cm.)	25 ft. (7.62 m.)	190	220
14 in. (35.5 cm.)	10 ft. (2.54 m.)	105	125
13.5 in. (34.3 cm.)	10 ft. (2.54 m.)	126	150

SUGAR MAPLE			
27 in. (68.6 cm.)	25 in. (76.2 cm.)	174	190
25 in. (63.5 cm.)	40 ft. (12.2 m.)	140	190
21 in. (53.3 cm.)	12 in. (30.5 cm.)	120	130
21 in. (53.3 cm.)	27 in. (68.6 cm.)	176	190
21 in. (53.3 cm.)	20 in. (50.8 cm.)	160	180
20.5 in. (52.1 cm.)	29 in. (73.7 cm.)	134	160
20 in. (30.8 cm.)	33 in. (83.8 cm.)	150	160
18 in. (44.7 cm.)	20 in. (50.8 cm.)	182	200
18 in. (44.7 cm.)	20 in. (50.8 cm.)	168	185
16 in. (40.6 cm.)	22 in. (55.8 cm.)	158	175
14 in. (35.5 cm.)	24 in. (61.0 cm.)	126	140
13 in. (33.1 cm.)	28 in. (71.1 cm.)	129	145
13 in. (33.1 cm.)	32 in. (81.3 cm.)	100	115

HEMLOCK			
22 in. (55.8 cm.)	20 in. (50.8 cm.)	164	175

A comparison of these tree sizes with the sizes of standing trees (Table 8) in the area shows that 39 per cent of the beeches and 13 per cent of the sugar maples making up this forest are as large, or larger, than the largest of which the annual rings were counted. This would indicate the age of the present forest to be well over 250 years.

The span of life of the sugar maple in this location seems to be determined by its size in relation to the soil. The humus is shallow, and the compact character of the subsoil seems to restrict the roots of this species to the soil above it—usually a matter of about 12 inches (30.5 cm.). Apparently few sugar maples above a certain size limit can long maintain them-

selves in this shallow soil against such severe wind storms as sometimes visit this forest. On the other hand, the life span of the beech seems to be determined by its susceptibility to fungus attack. There is probably no large beech tree in the area which is not hollow, at least at the base, the heartwood having been reduced to punk by the various species of fungi which seem to find an easy entrance to the tissues of this species. When finally the sapwood is affected, the tree will ultimately be twisted off its base by a wind storm, leaving the hollow stub standing. Apparently about 250 to 300 years is the limit of life for either the beech or the sugar maple in this location. There is need, therefore, for continual replacement of the dominants to make good the losses which more or less regularly occur.

The foregoing facts, taken together, clearly warrant the conclusion that in the area under study a gradual change in the status of the forest components has been in progress for some time, and the forces operating to bring about this change are operating at the present time. The conclusion that the hemlocks are being displaced by the beech and the sugar maple is inescapable. That the hemlocks formerly occupied much more territory than they now do is indicated by their remains in an area now completely occupied by the beech-maple association. In this movement the beech seems to play the leading part. Not only may beech hinder germination of hemlock by creating a humus unfavorable to the development of hemlock seedlings, but it may, by its dense shade, prevent the normal development of young hemlocks beneath its canopy, or by root competition in dry seasons reduce soil moisture available to neighboring hemlocks to the point where it ceases to be sufficient for hemlock requirements. The fact that beech roots more deeply than sugar maple in this environment may better fit it to play the part of entering wedge in displacing hemlock here. However, it may be expected that sugar maple will be more largely represented in this location in the future than it is now.

The need of plants for light is preëminent. Zon and Graves (1911) point out that early in life all plants are more or less tolerant of shade, but as they increase in size, their requirements for light become more and more definite, and that these requirements differ for different species. Burns (1923), studying the light requirements for 14 species of forest trees, found that each had a specific minimum requirement below which it could not live. The three trees with the lowest requirements he found to be, sugar maple lowest, beech next, and hemlock next. Daubenmire (1930), studying evaporation rate, light, soil acidity, and soil moisture under hemlock in Indiana, attempted to correlate the difference between hemlock and beech-maple. The results indicated an equal degree of mesophytism in the two associations. Studies of hemlock and its environment have been made by Moore, Richards, Gleason, and Stout (1924). While some slight differences were

found in the evaporation rate and in soil and air temperatures as compared with the hardwood forest, these do not seem significant enough to be recognized as controlling factors in the distribution of hemlock.

Apparently hemlock is not restricted in its location, as compared with the adjacent beech-maple association, by either temperature or moisture conditions, or by the chemical constitution of the soil; but rather, it is in process of elimination by competition within areas formerly occupied by it but now being gradually taken over by beech and sugar maple as dominants. The view that hemlock is thus being displaced is in accord with the opinion expressed by Weaver and Clements (1929) that the hemlocks of this region represent a remnant of the so-called "Lake Forest" to the north, returning with the retreat of the glacial ice, and now existing here only as small relict areas.

The fact that no chestnut saplings, and but very few smaller chestnut trees are to be found within the area, and that chestnut and hemlock were formerly very closely associated (Fig. 9) apparently on more or less even terms, leads the writer to the opinion that chestnut as well as hemlock would have fallen in competition with the beech-maple association, had not the "chestnut blight" wiped out the chestnuts before their time. For this reason chestnut may not be expected to "come back" in this environment naturally.

Undoubtedly the few oaks, hickories, sassafras, and other trees of sub-climax types will gradually be eliminated through failure of reproduction, though sassafras has the great advantage of being able to reproduce by suckers from the roots. The presence of these trees, normally associated with the oak-chestnut forest, suggests an inter-relation of hemlock with oak-chestnut on the one hand, and beech-maple on the other, such as might have produced at one time an oak-chestnut-hemlock mictium which has now gone over to beech-hemlock.

That cucumber, and probably tupelo, have suffered displacement from the interior forest is clear, yet because of the steady though small reproduction rate of both species, and their commanding size when fully grown, they will probably continue for a long time as associates with the climax.

Secondary Succession

Under present conditions, the causes of secondary succession within the area are limited to denudations occurring by reason of the washing away of humus and top-soil at times of heavy rains, the slipping of earth and shale on the sides of the ravines due to erosion, and to the letting in of sunlight where breaks in the forest canopy occur because of the death of large trees which may either fall or remain standing, or whose tops or large branches may be broken off.

It is the uprooting of the large trees, exposing a more or less circular area of hard yellow clay, that causes most if not all of the secondary succession noted in the area by the writer. Such a depression may hold water for a large part of the year, and for this reason many seeds will not germinate upon it. From the edges of the torn mat of humus pokeweed is usually the first plant to appear. Commonly red-berried elder and high-bush blackberry are found along with the pokeweed. On the bare wet clay the spores of ferns, and the seeds of violets, wood sorrel, and great lobelia will germinate. Tulip and white ash frequently appear, but neither beech nor sugar maple will start on this surface.

From studies which have been started within the area in several localities where secondary succession is in process, but which cannot be reported on in detail here, it appears that tulip and white ash are the species that thrive, when the opportunty offers for rapid development in unoccupied territory. This accounts for the rather general distribution of these two species throughout the climax, both at the present time, and in the case of the tulip, formerly.

ECOLOGICAL CLASSIFICATION OF PLANTS

The dominant plants in any biotic community are considered to be those which, by reason of their size, abundance, and distribution, largely determine the conditions under which other organisms shall live in association with them. In the forest the dominants are usually trees. They are exposed directly to the sun, rain, snow, and wind; and other organisms mostly live underneath them. Beneath the trees temperature, light, evaporation rate, humidity, precipitation, wind, and other factors in the environment may be greatly modified. Only such plants and animals as are adapted to life under these conditions can exist here. The dominants therefore not only raise barriers against certain forms of plant and animal life—they invite others.

Primary dominants are those which, by reason of their wide and more or less even distribution and abundance, exercise their influence over the greater part of the community. Secondary dominants are those dominants which, by reason of their less frequent occurrence, do not exercise as great influence over the community as such. Their occurrence in the community, however, is rather regular. Incidental dominants, in this paper, are such trees as attain large size, and so exert an influence over a limited area, but which do not occur in numbers, or with any degree of regularity in the community. Subdominants are all other plants. They do not attain great size, but have adapted themselves to conditions of existence below the dominants. On this basis the plants of the area may be classified as in Table 10.

TABLE 10. Ecological classification of plants.

In beech-maple association	In beech-hemlock-oak-(chestnut) mictium	In ravines (flood-plain extensions)
1. Primary dominants		
Beech Sugar Maple	Beech Hemlock (Chestnut)	Hemlock
2. Secondary dominants		
Red Maple Tulip White Ash Northern Fox Grape	Red Maple Red Oak	
3. Incidental dominants		
Shagbark Hickory Cucumber Red Oak White Oak	Shagbark Hickory Cucumber Tupelo Sassafras White Oak Wild Black Cherry Pignut Black Birch Scarlet Oak	American Elm Basswood Slippery Elm Butternut Black Walnut Bitternut
4. Sub-dominants		
Hop Hornbeam American Hornbeam Shrubs, vines, herbs, ferns, and other plants, as listed in tables 6 and 7.	Hop Hornbeam American Hornbeam Flowering Dogwood Shadbush Shrubs, vines, herbs, ferns, and other plants as listed in tables 6 and 7.	Shrubs, vines, herbs, ferns, and other plants.

CHARACTER OF ANIMAL POPULATION

METHODS OF STUDY

Contrasted with the study of the plants of any area the study of its animal population presents an entirely different and much more difficult problem. Animals do not "stay put" as do plants. If the ecologist would really learn to know the animal content of an area, he must become so familiar with it that he feels thoroughly "at home" in it, and should achieve, in some degree at least, such a sympathetic attunement to the ebb and flow of its life activities that he becomes conscious of changes while they are in progress, and senses the significance of small matters as they arise. He must acquire the ability to move quietly and easily about, making a minimum of disturbance, while the senses of sight, hearing, and smell bring him information for his record.

While the methods of study of animals in their natural habitats must vary in accordance with the season, and often with the species studied, there are some general methods which, if carefully followed, should always offer a fair chance of definite returns. Such general methods as were used by the writer in this study were:

1. Regular and frequent visitation of the area. The writer was fortunately so situated that he could and did devote the Mondays of each week throughout the entire four years of this study to such visitation, with the exception of six scattered weeks, when observations were made by others under his direction. Familiarity with the area and its inhabitants was thus built up, and a picture of consecutive changes as they occurred secured, which probably could have been realized accurately in no other way. In addition to these extended weekly observations it was often possible to augment the record by more limited occasional visits in connection with other matters.

2. An increasing keenness of observation and interpretation of things seen and heard was deliberately sought after. A bird's feather on the ground, the scattered remnants of a meal, a dead shrew on a log, the droppings of animals, the barred owl's cast pellets, the character of woodpecker "workings," and many sounds and smells, all raised questions for which the correct answers were sought, even though considerable time might elapse between question and answer, and sometimes experiment was necessary for the solution of the problem.

Thus the presence of a heretofore unsuspected mammal (later confirmed by securing two specimens in the flesh) was determined through the discovery of the tiny jaw bone of the smoky shrew; and a method of ascertaining the presence of the seldom-seen flying squirrel was worked out by feeding hickory nuts to several species of captive squirrels, and noting that the flying squirrel, (and in fact the other species also) left a characteristic "signature" upon the nut shell.

3. Orderly routine in observation and recording on the spot. On each weekly visit the same course was followed, covering the entire area. Frequently the direction of travel was reversed, so that the same part of the area might be visited at different times. During this weekly survey an effort was made to identify accurately each species seen or heard; to make as complete a count of individuals as possible, or in the case of large numbers, to make a close estimate of numbers based on unit counts; to locate the occurrence of each individual on a small map carried for the purpose each week; to make notes of conditions of weather, changes in the plant or animal life observed, activities, relationships, or other facts considered significant. As this work was, with the few exceptions noted, always performed by the same person, usually alone, differences which might be due

to individual variances were eliminated, and the resultant data should be fairly comparable from one period to another.   In estimating populations which are not restricted either to beech-hemlock or beech-maple environment, account does not have to be taken for what Leopold (1933) calls "blanks," as the entire area is essentially "forest" throughout.   Even the area of the trails does not have to be figured out, as these are a very much used part of the habitat.   All observations were recorded under appropriate headings on a temporary record carried for the purpose, and later transcribed to a permanent record, usually on the evening of the same day.

4. Concentration, at times, on special phases of animal behavior.   Such were the studies of animal tracks in the snow, the location of the nesting territories of birds, and the home ranges of mammals, the study of food habits as special opportunities presented themselves, and the special study of the abundance and distribution of mice and shrews.

5. Visitation of the area at night.   As the activities of some animals are carried on mainly after dark, it was considered of importance to visit the area a number of times, for varying periods, during the hours of darkness.

6. Observation of captive animals.   While it is recognized that animals in captivity undoubtedly behave differently than in a state of natural freedom, it is also evident that much may be learned as to the character of the animal, and some understanding gained as to its equipment to meet competition in its natural environment, from a study of it at close quarters, even though under restraint.   Opportunities were at hand during the summers to thus become acquainted with the New York weasel, raccoon, opossum, skunk, woodchuck, cottontail rabbit, red squirrel, chipmunk, flying squirrel, white footed mouse, pine mouse, barred owl, Cooper's hawk, red-tailed hawk, red-shouldered hawk, crow, and pilot blacksnake.

THE MAMMALS OF THE AREA

Table 11 gives the list of mammals whose presence in the area is known from direct observation.   Representatives of all of these except the Virginia deer and the fox squirrel have been in the hands of the writer at various times, and skins of all of the species of mice, shrews, moles, bats, and chipmunk are deposited with the Cleveland Museum of Natural History.   Scientific names are as given in the List of North American Recent Mammals, Bulletin 128 of the United States National Museum, with the exception of the eastern chipmunk, which is described by Howell (1929).

While the numbers and relative abundance of mammals in the area will always be subject to considerable fluctuation, the common species listed in Table 11 will usually be found in the order given; the most abundant being placed first.   For the less common species enough information is not yet at hand to warrant an attempt to estimate abundance.

TABLE 11. The mammals of the area.

Common species

Short-tailed Shrew	*Blarina brevicauda talpoides* (Gapper).
Northern White-footed Mouse	*Peromyscus leucopus noveboracensis* (Fischer).
Eastern Chipmunk	*Tamias striatus fisheri* Howell.
Northern Gray Squirrel	*Sciurus carolinensis leucotis* (Gapper).
Southern Red Squirrel	*Sciurus hudsonicus loquax* Bangs.
Small Eastern Flying Squirrel	*Glaucomys volans volans* (Linnaeus).
Cottontail Rabbit	*Sylvilagus floridanus mearnsi* (Allen).
Southern Woodchuck	*Marmota monax monax* (Linnaeus).
Eastern Raccoon	*Procyon lotor lotor* (Linnaeus).
Eastern Skunk	*Mephitis nigra* (Peale and Beauvois).
Virginia Opossum	*Didelphis virginiana virginiana* Kerr.
Eastern Red Fox	*Vulpes fulva* (Demarest).
Domestic Dog	
Domestic Cat	

Less common species

Smoky Shrew	*Sorex fumeus fumeus* (Miller).
Hairy-tailed Mole	*Parascalops breweri* (Bachman).
Star-nosed Mole	*Condylura cristata* (Linnaeus).
Silver-haired Bat	*Lasionycteris noctivagans* (Le Conte).
Big Brown Bat	*Eptesicus fuscus fuscus* (Beauvois).
Red Bat	*Nycteris borealis borealis* (Müller).
New York Weasel	*Mustela noveboracensis noveboracensis* (Emmons).
Fox Squirrel	*Sciurus niger rufiventer* (Geoff.).
Pine Mouse	*Pitymys pinetorum scalopsoides* (Audubon and Bachman).
Meadow Mouse	*Microtus pennsylvanicus pennsylvanicus* (Ord).
Hudson Bay Jumping Mouse	*Zapus hudsonius hudsonius* (Zimmerman).
Woodland Jumping Mouse	*Napaeozapus insignis insignis* (Miller).
Virginia Deer	*Odocoileus virginianus virginianus* (Boddaert).

The above list of 25 mammals (omitting dog and cat) contains 49 per cent of the entire list of mammals (51) listed by the Ohio Department of Agriculture as now to be found in the State (Bull. 54, Bureau Scientific Research, 1931).

That the bison (*Bison bison* (Linnaeus)), American elk (*Cervus canadensis canadensis* (Erxleben)), Virginia deer (*Odocoileus virginianus virginianus* (Boddaert)), black bear (*Ursus americanus americanus* (Pallas)), and panther (*Felis cougar* Kerr) were once abundant in this region is attested by early writers. In view of the fact that all of these animals were completely exterminated from northern Ohio many years ago, it is interesting to find evidence of the return of one of them, the Virginia deer, to the locality. In view of the present overstocked condition of the deer ranges in western Pennsylvania (Clepper 1931) it would not be surprising to find deer wandering into northeastern Ohio from that direction.

DISTRIBUTION AND ABUNDANCE OF MAMMALS

In late July and early August 1932 some line trapping with spring mouse traps throughout the area demonstrated the very general distribution of short-tailed shrews and white-footed mice in all parts of the forest. It appeared that a catch could be made at every stump, or decaying log, or litter of sticks. Tunnels and runways were also found everywhere under the humus and

loose leaf-litter. Apparently the habitat was then occupied to the saturation point by mice and shrews. From a third to a half of the 98 animals trapped were either wholly or partially eaten, though the traps were inspected daily, and were usually under cover. This in itself indicated a large shrew population. The conditions of that autumn have not been duplicated since.

In late September and early October of the same year a more definite attempt was made to secure data that could be used as a basis for estimating the number of these two animals. Five quadrats were laid out in carefully selected territory, each 10 meters (32.75 feet) square. The location chosen for each was such as to make it typical of the whole area. Two were in beech-hemlock environment, and three were in beech-maple. One of the three in beech-maple environment had in it no stumps or logs or cover of any kind except the humus and leaf litter of the forest floor. The others included various types of shelter such as are commonly distributed over the area—tree roots, old logs, stumps and the like. Mouse traps of the usual spring-catch variety were used, baited with both oatmeal and raw beef, and usually set in groups of threes in runways that showed evidence of use, or in sheltered places. Trapping in each quadrat was continued until several days had passed without a catch. Usually this meant about two weeks of total time. It was then assumed that all of the mice and shrews using the quadrat as a hunting ground had been captured. Traps were inspected daily, often more frequently. Careful records were kept.

If the average catch of all five quadrats is taken as representing the population of an average 10 meter square for the whole area, then the population may be computed for any unit of the area. Later studies (unpublished) made by Mr. B. P. Bole, Jr., of the Cleveland Museum of Natural History, have demonstrated that the drift of small mammals from neighboring territory into the quadrat, especially at times when populations are high, is greater than was realized at the beginning of this study. It was originally felt that an offset existed in the loss of animals eaten and removed from the traps, large enough to counterbalance the entrance of others into the quadrat during trapping operations. The figures given in Table 13 for short-tailed shrews and white-footed mice are therefore undoubtedly too high, yet they are used in this paper as they establish a basis for comparisons with subsequent years during which the same trapping methods have been followed.

Accordingly, in September 1933 five quadrats of the same size as those used in 1932 were set up adjoining the quadrats of 1932, and trapped. The original five quadrats were again trapped in the autumn of 1934, and again in the autumn of 1935. Four consecutive groups of annual records were thus provided. In addition to indicating the distribution and abundance of short-tailed shrews and white-footed mice, these operations revealed the

presence of certain other species of small mammals—namely, Hudson Bay jumping mouse, woodland jumping mouse, pine mouse, meadow mouse, smoky shrew, and star-nosed mole. The results of the quadrat trapping are given in Table 12.

TABLE 12. Trapping records of mice and shrews.

Quadrats	A-beech-maple				B-beech-hemlock				C-beech-maple				D-beech-hemlock				E-beech-maple				Totals			
Years	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35	'32	'33	'34	'35
Short-tailed shrew	10	4	2	8	12	0	0	2	5	3	1	4	6	2	1	5	4	3	2	4	37	12	6	23
White-footed mouse	8	1	0	3	3	0	0	5	6	0	0	4	5	3	1	7	6	1	3	8	28	5	4	27
Hudson Bay jumping mouse										1									1				1	
Woodland jumping mouse						1												1				1		
Pine mouse										2	5								2				2	7
Meadow mouse								1																1
Smoky shrew			1			1																	2	
Totals	18	5	3	11	16	0	1	8	11	3	3	13	12	5	2	12	10	4	5	14	67	17	14	58

By reducing square meters to acres, and averaging the catch of all five quadrats annually for shrews and mice, an estimate of the numbers of these animals on an acreage basis may be secured. These figures are shown in Table 13. For convenience the estimated numbers of the other common mammals of the area are also shown in this table. These are based, not on trapping records, but on weekly counts of numbers, studies of tracks on the snow in winter, and other evidence. The fact that the two species of jumping mice do not appear from the trapping records to be of general distribution within the area, and the actual limits of their habitats being unknown at the present time, makes it impossible to include these species in the estimate. The occurrence of the meadow mouse in 1935 is considered not to represent a resident animal, but rather one migrating through the area. The four records of the occurrence of the smoky shrew (2 in traps, 1 jaw-bone found, remains of 1 in an insect trap) at widely separated points, two of which were in beech-hemlock, and two in beech-maple environment, suggest the general distribution of this animal throughout the area, and estimates of numbers are given. The case of the pine mouse presents an interesting situation. Previous to 1934 there was no evidence of the presence of this species in the area. The capture of 2 individuals (1 female, 1 immature male) in one quadrat well within the interior forest (beech-maple) in 1934 indicated small numbers and limited distribution. In 1935, although but 7 captures were recorded in the quadrats (Table 12), 12 others were caught in various ways (the writer caught one by hand) at such widely separated points within the area as to make it certain that the species was then well established in all parts of it.

TABLE 13. Common mammal population of the area—numbers of individuals.

Species	Autumn 1932			Autumn 1933			Autumn 1934			Autumn 1935		
	Per acre	*Per hectare	Total in area	Per acre	Per hectare	Total in area	Per acre	Per hectare	Total in area	Per acre	Per hectare	Total in area
Short-tailed shrew....	299.45	739.6	19464.	97.12	239.8	6312.	48.56	119.9	3156.	187.	461.8	12165.
White-footed mouse.	218.52	539.7	14203.	40.46	99.9	2629.	32.37	79.9	2104.	209.8	518.1	13635.
Pine mouse..........	....	....	.. ..	....	....	....	8.1	19.8	525.	24.2	59.7	1575.
Chipmunk	10.0	24.7	650.	4.0	9.9	260.	10.0	24.7	650.	15.0	37.0	975.
Smoky shrew........	......	....	.. ..	....	....	....	8.1	19.8	525.	4.0	9.8	260.
Gray squirrel.......	0.03	0.07	2.	0.31	0.74	20.	0.9	2.2	60.	1.0	2.4	65.
Red squirrel........	0.31	0.74	20.	0.23	0.57	15.	0.31	0.74	20.	0.5	1.2	30.
Cottontail rabbit.....	0.46	1.14	30.	0.61	1.48	40.	0.03	0.07	2.	0.06	0.15	4.
Flying squirrel.......	.. .	....	....	..	....	......	0.37	0.91	24.	0.37	0.91	24.
Woodchuck....... ..	0.15	0.37	10.	0.06	0.14	4.	0.09	0.22	6.	0.06	0.15	4.
Raccoon........ ..	0.18	0.45	12.	0.15	0.37	10.	0.18	0.45	12.	0.18	0.45	12.
Opossum	0.03	0.07	2.	0.06	0.14	4.	0.03	0.07	2.	0.03	0.07	2.
Skunk.	0.09	0.22	6.	0.09	0.22	6.	0.00	0.00	0.	0.00	0.00	0.
Red fox...	0.03	0.07	2.	0.06	0.14	4.	0.01	0.03	1.	0.03	0.07	2.
Totals per acre ..	529.25	....	... ..	143.15	.....	.....	109.05	.....	... ..	442.23	..	......
Per hectare.......	.	1307.13	....	....	353.40	.....	.. ..	268.79	. ....	.....	1091.80	.....
Total in area ...	... ..	.... ..	34401.	.	..	9304.	..	.	7087.	..	.	28753.

*1 hectare = 2.47 acres.

The status of the moles and the bats in the area is not clear. The subsoil is ill-suited to the work of moles because of its hardness, and though earthworms are noted in the humus and in the soft wood of decaying logs, the tunnels of moles are rarely evident. Perhaps the loose leaf-litter may effectually conceal them. On the other hand, when the humus was reduced to the semblance of tinder during the dry spring and summer of 1933 and mole tunnels were for the first time noted in the drying stream-beds, they were few in number. For the present the writer assumes that the numbers of moles of all species in the area are quite limited. But two specimens have been taken, representing two species.

The bats are as elusive as the moles. Bats have never been noted in numbers, and only on the wing. They give the impression of passing over or through the area rather than of hunting within or over it. They are usually seen flying high, though Mr. Earl Cady reports having seen two large bats (big brown bats?) at 12:30 A.M. September 7, 1933, apparently busily feeding in the moonlight over a large patch of jewel-weed in the woods. In the latter part of August 1933 an attempt was made to determine at least the species of bats flying in the forest. Mr. Arthur B. Fuller of the Cleveland Museum of Natural History, on three different nights, by wing-shooting over a grape tangle in the beech-maple association, collected a total of 5 bats, of which 3 were big brown bats. Apparently this species is the common bat of the area.

FOOD CHAINS AND ECOLOGICAL NICHES

In summing up the relative importance of the mammals of the area account must be taken not only of their numbers, but also of the duration of the periods of their activity, and of their food-habits. Those mammals classed as the less common species (Table 11) are clearly of much less importance ecologically than are the common ones. If they were entirely removed from the area the probability is that little if any change would be apparent. Attention may therefore be centred upon the common species. Table 14 classifies these on the basis of duration of activities.

TABLE 14. Common mammals classified according to duration of activities.

	Active through-out the year	Active by day	Active by night	Inactive during winter
Short-tailed shrew......	*	*	*	.....
White-footed mouse....	*	.....	*	.....
Chipmunk.............	.....	*	.....	*
Gray squirrel..........	*	*	.....	.....
Red squirrel...........	*	*	.....	.....
Flying squirrel.........	*	.....	*	.....
Cottontail rabbit.......	*	*	*	.....
Woodchuck............	.....	*	.....	*
Raccoon..............	.....	.....	*	*
Skunk................	.....	.....	*	*
Opossum.............	.....	.....	*	*
Fox..................	*	*	*	.....

Probably the most ceaselessly active of these animals is the short-tailed shrew, though Shull (1907), who studied the habits of this mammal, expresses the opinion that "times of daylight are not selected by the shrew for its greatest activity." Yet the writer's observations do indicate considerable daylight activity for this little mammal. In the area under study the barred owl is a consistent hunter of the shrew by daylight. One can often locate shrews at work by the rustling movement of dry leaves on the forest floor by day as well as by night. Not infrequently one gets a glimpse of a shrew by day as he flashes from one opening of his tunnel to another, or he may sometimes be surprised at work by quickly removing or turning over the decayed log or piece of bark that serves as a roof for his runway. Traps set in the morning and inspected before dark frequently contain shrews. Sometimes the bait will be so quickly taken by shrews, after setting the trap in daylight, that the operator hears the snap as he turns away. That shrews are active at all seasons of the year is indicated by their tunnels under the snow, and their trails on its surface in winter.

Although the shrew is usually referred to as an insectivore, ecologically he might just as well be classed as a carnivore, for he is a hunter after fresh meat in any form, and in proportion to his size he needs a great deal of it. Shull (1907), studying the short-tailed shrew in a swampy habitat near

Ann Arbor, Michigan, found that in winter snails formed a part of the food supply. Meadow voles *(Microtus)* were also an observed part of the diet. It was found that vegetable foods offered to captive shrews were invariably rejected.

On the basis of experiments with captive shrews, Shull estimated that one short-tailed shrew, in one month, will eat:

	Number	Per cent of total
Meadow mice or equivalent in mice	8	40
Adult insects (size of May beetles — Lachnosterna)	90	20
Insect larvae (size of May beetles — Lachnosterna)	78	20
Earthworms 4 cm. long, contracted	53	5
Snails	18	15

In a different habitat the relative availability of the different items in the diet would certainly influence the proportions consumed. At North Chagrin undoubtedly the proportion of mice eaten would run higher both in number and per cent of total, as *Peromyscus* is smaller than *Microtus,* and the supply of snails would be considerably less. It is also probable that the proportion of insects, millipeds, and the like would run higher. Smaller shrews, like *Sorex,* would also be preyed upon. It is important to recognize the short-tailed shrew as more than an eater of insects.

Occupying the position of the most abundant mammal in the area, being the only one that approaches constant activity by day and by night, and at all seasons of the year, requiring an enormous amount of animal food at all times, and having no real check upon numbers except the barred owl, the short-tailed shrew appears as probably the most influential mammal in the area. He acts as an efficient check upon the numbers of mice and other species of shrew, and takes out the humus and decaying logs and stumps an immense number of insects and their larvae and of other forms like millipeds, centipedes, sowbugs, and worms. It is not entirely fanciful to liken his network of under-cover tunnels and runways to a vast system of spiderwebs, laid down for the same purpose as the spider's web—the ensnaring of his prey.

From the standpoint of numbers and all-year-round activity the white-footed mouse probably ranks second in importance in the area. Compared with the shrew, the white-footed mouse does not exhibit the same kind of high-tension activity. Johnson (1926) found experimentally that forest deer mice *(Peromyscus)* were nocturnal, with a well marked rhythm of activity, sinking to a minimum during daylight hours and reaching a high degree normally during the hours of darkness. Unlike the shrew, the mouse is directly dependent upon plant products for his main support. Although a rodent, he is not a strict vegetarian, however, but consumes considerable animal material. All of the captive white-footed mice observed by the

writer have always eagerly accepted insect food. Snails also are probably eaten (Cahn and Kemp, 1929).

Checks upon undue increase in numbers of mice exist in the short-tailed shrew, as noted above; the barred owl, whose cast pellets found in the area frequently contain remains of *Peromyscus;* and in the larger mammals of the flesh-eating group—skunk, raccoon, opossum, weasel, and fox.

The chipmunk should undoubtedly be placed third in importance among the mammals of the area on the basis of number and general distribution, even though he withdraws from above-ground activities at certain seasons of the year. While popularly credited with being a complete hibernator (Anthony, 1928, p. 243), this is certainly not the case with the chipmunks in the area under study. Except for the winter 1932-33, when the chipmunk population at North Chagrin was reduced to a very low ebb, the writer has observed chipmunks abroad throughout the winter months, sometimes with the temperature as low as 10° F. (-12.2° C.), and has noted their tracks in the snow indicating great activity at certain times in winter. Counts of as many as 58 in one morning, and 63 in another, both in February, suggest anything but complete hibernation at that time. In fact the writer is of the opinion that the entire chipmunk population was aroused to a high pitch of excitement by mating activities at that particular time.

The periods of the chipmunk's greatest activity at North Chagrin are from the first week in May to the middle of July, and from the middle of September to late November if the weather is good. There is a period of retirement underground from mid-July through August which is probably correlated with the physiological condition of moulting and renewing of the pelage. Howell (1929) mentions the fact that out of 1,349 specimens of *Tamias* examined by him, very few moulting specimens have been found. This is no doubt due to the animal's disappearance during the period of moult, so that relatively few moulting specimens would be encountered by collectors. Schooley (1934) thinks this disappearance, reported by others but not observed by him, is due to the summer breeding season.

The chipmunk, like the mouse, is dependent mainly on vegetable matter for his food supplies but also takes animal matter (Howell 1929, Cahn and Kemp 1929, Seton 1909). Captive chipmunks observed by the writer ate with great avidity all insects offered, and shells of snails are commonly found among the refuse on their feeding tables. In May and June the chipmunks at North Chagrin do a great deal of "rooting" in the humus after such food as the tubers of spring beauty, dwarf ginseng, Indian cucumber, and squirrel corn, or the root-stocks of trillium. In the fall, beech nuts, sugar maple seeds, and other nuts and seeds are gathered and stored underground.

Checks on the numbers of chipmunks in the form of larger predators

are not very apparent.   It is possible that the fox and the weasel may exercise some influence, but direct evidence is lacking. Chipmunk remains have not been found in the casts of the barred owl in the area, nor has the owl been observed to hunt chipmunks.   Cats have been definitely observed stalking chipmunks.   Possibly the pilot blacksnake may be a definite consumer of chipmunks in summer.   Under favorable conditions of food supply there seems to be no reason why the chipmunk population should not occupy all available habitats in the area—and this indeed seems frequently to be realized. Competition would then act to prevent overpopulation.

The other squirrels—red squirrel, gray squirrel, and flying squirrel—are all consumers of nuts, seeds, and fruits, as well as of some animal matter. Captive flying squirrels and captive red squirrels, under the observation of the writer greedily ate all insects offered them.   As a group the arboreal squirrels are important members of the community by reason of their almost continuous activity throughout the year and their steady consumption of basic forest food supplies.   Their function as destroyers of large numbers of insects must not be overlooked.   Competition between species and individuals apparently acts as an efficient check upon numbers.

The rabbit and the woodchuck are normally rather unimportant elements in the biota of the area because of their small numbers.   If either should increase greatly in abundance, and maintain their increased numbers for any considerable period of time, they might have a significant relation to the vegetation of the area by reason of their food requirements.   The rabbit especially, under such conditions, might affect greatly the character of forest seedling trees and saplings.   Such a condition has apparently never occurred, however.   The very apparent check upon both of these animals is the red fox, about whose dens the remains of woodchucks and rabbits are very commonly found.   Hamilton (1935) mentions rabbits as constituting 22.1 per cent by bulk, of the food of 206 foxes in fall and winter in New York and New England, and woodchuck remains stand highest in the list for 31 fox dens examined by him in July and August.

With the exception of the short-tailed shrew, the carnivores of the area have a larger sphere of activity than the 65 acres under study.   Yet their regular visitation of it, and their resident character to some extent in the case of certain individuals, means a very considerable influence in its biotic relationships.   The raccoon, the skunk, and the opossum may be regarded as somewhat in the nature of additional checks upon the undue increase of the smaller mammals.   They undoubtedly limit to some extent the numbers of birds nesting on or near the ground.   They must also be recognized as large consumers of insects, and of the so-called "cold-blooded" animals—crayfish, frogs, salamanders, and snakes.   Their periods of greatest activity

correspond with those of the "cold-blooded" animals, and raccoons are espe-
cially diligent hunters of this sort of fare.

The weasel and the fox provide still further checks upon the smaller
mammal population, and the fox especially seems important in limiting the
number of rabbits.

Taken as a group, the mammals of the area illustrate well the adapta-
tions of animals to a forest environment. Omitting the dog and the cat,
which are associated with the presence of man in the near vicinity, and the
deer, which is an occasional visitor only, and the meadow mouse, which we
may consider a transient visitor, it appears that the 23 species remaining
consist of 5 squirrels, 4 mice, 1 rabbit, 1 woodchuck (all chiefly herbivores) ;
2 shrews, 2 moles, 3 bats (all chiefly insectivores) ; and the raccoon, opos-
sum, skunk, weasel, and fox (all chiefly carnivores). The composition of
the whole group then, may be roughly indicated as:

Herbivores, 48 per cent.

Insectivores, 30 per cent.

Carnivores, 22 per cent.

This arrangement, however, is only a species grouping and does not indi-
cate food relationships with any degree of exactness. Probably the weasel
is the most nearly strictly carnivorous animal on the list, and the rabbit and
the woodchuck the most nearly strictly herbivorous ones. Undoubtedly the
squirrels and the mice consume great quantities of insects along with their
mainly herbivorous diet, and this is true also of most of the carnivores.
Even the red fox is accredited as an insect eater (Dearborn, 1932, and Ham-
ilton, 1935). The bats, no doubt, are strictly insectivorous, but the moles
and shrews are carnivorous as well as insectivorous. Most of those classed
as carnivores might also be classed as omnivores. But the gist of the mat-
ter is that plant products, insects, and other invertebrates, are the mainstay
of the mammal population of the area, while to a more limited extent the
smaller mammals themselves serve to support the larger ones.

In their occupation of the territory it is interesting to see how these
mammals have occupied fully all available habitats. The moles occupy the
deeper parts of the substratum, so far as it is available to them; the shrews
have appropriated the loose humus and leaf litter of the forest floor, using
the runways of mice and moles as well; the chipmunks are animals of the
floor itself and the débris that lies upon it in the shape of old logs, stumps,
and litter, though making their homes and storehouses in tunnels that reach
into the subsoil itself; the mice are inhabitants of logs and stumps and hol-
low trees and other forest litter, and the white-footed mouse is a climber
of trees as well; the red squirrel, with his headquarters usually under some
stump or bunch of roots, also ascends the trees, and frequently builds a nest
in a grapevine suspended aloft; the gray squirrel is the true arboreal animal

of the area, spending much time aloft, using aerial runways by preference, and having his winter quarters usually high above the ground in some hollow tree top; the flying squirrel is also an arboreal animal, extending his aerial highways beyond the limits of those of the gray squirrel by reason of his abilities as an aerial glider; and the bats complete the occupation of all available habitats by hunting through the air itself.

The larger mammals of the list are mainly hunters upon the surface of the ground, though the raccoon and the opossum are climbers, and the raccoon's winter quarters are usually high above ground.

This division of territory and diversity of diet makes possible the support of a large population of mammals adapted to the limitations of the habitat, provided basic food supplies are present in normal quantities. In this particular forest this means beech nuts, sugar maple seeds, herbaceous vegetation, insects and other invertebrates.

Such was the condition in the autumn of 1931. At that time apparently every available habitat within the area was occupied to its upper limit of capacity by the shrews, mice, chipmunks, and gray squirrels. There had been very large yields of beech nuts and sugar maple seeds the previous autumn, as well as this autmun. Food supplies were more than adequate for even the large population then occupying the territory.

FLUCTUATIONS IN NUMBERS OF MAMMALS

As Elton (1927) has pointed out, the chief cause of fluctuation in animal numbers is the unstability of the environment. This is well illustrated in the case of the area under study by what happened in the autumn of 1932. This was the time of almost complete failure of the beeches and sugar maples to produce seed. Whether the resting rhythm of these two trees normally coincides, or whether it does so only occasionally because of a difference in length of rhythm, remains for further studies to determine. At any rate, basic food supplies practically disappeared just before the winter of 1932-33.

There was little storage of food by chipmunks that autumn, and they went underground almost a month earlier than the previous year when storage activities ran well into the last of November. Although there was no observation of the activities of the white-footed mice, the absence of their accustomed food supplies would have produced more or less of the same condition with them, so far as storage of winter food was concerned. The red squirrels, as appeared later, gathered and stored large quantities of tulip seed cones, and some of them subsisted upon scarcely anything else during the entire winter, as indicated by the refuse about their middens as the winter progressed. Hemlock seeds were also used by the red squirrels, but there was a deficiency in yield of these seeds also. Mushrooms were

much used.   Seeds of cucumber trees, usually shunned as articles of diet,
were freely gathered, stored and eaten by red squirrels that winter.   These
animals are probably naturally resourceful in the discovery and use of
foods outside the usual list, as the droppings of horses were twice noted
in red squirrel middens.   These must have been discovered and brought in
from near-by bridle paths.   The fact that the red squirrels did not occupy
the territory as fully as did the other rodents was also in their favor, for
it is a recognized fact that competition within the ranks of a species is al-
ways keener than between different species, as the needs of the individuals
are then identical.   But the red squirrels were able to and did expand their
individual territories, spreading into parts of the area not previously oc-
cupied by them.

The gray squirrels left the area early.   About 50 of these animals oc-
cupied the area the previous winter, producing enough young in spring to
keep their numbers fairly constant.   But in September they moved out,
leaving one lone squirrel to face the famine alone.   This individual was
frequently noted during the winter following.   He seemed to be subsisting
on a few hickory nuts, red oak acorns, tulip seeds, and mushrooms.   The
writer even saw him sampling the hard woody bracket of *Polyporus ap-
planatus*, and later noted that the marks of squirrels' teeth on these un-
palatable fungi were not at all uncommon that winter.

An interesting fact in connection with this winter was the increase in
numbers of cottontail rabbits within the area.   Previously they had been
noted about the edges of the forest.   Now they extended their feeding
grounds into all parts of the area.   Numbers were probably doubled, in-
creasing from 20 to 40, and there was much evidence of their activities in
the "barking" of young trees, and nipping off of the terminal buds and twigs
of thousands of small trees of beech, sugar maple, and red maple.   This
meant the destruction of many seedlings, but of course in most cases they
would necessarily have been eliminated by competition later.   The rabbits
naturally were not affected by the failure of beech nuts and sugar maple
seeds, as their food consists of bark, buds, twigs, and the green leaves of
the ferns, *Carex*, and other woodland plants such as *Hepatica* and *Dentaria
diphylla* whose leaves remain green all winter.

During this winter not a single chipmunk was seen above ground, where
counts of as high as 58 in a morning had been made the previous winter
and have been made since.   The following spring it was apparent that very
few chipmunks had survived the winter, as only a few individuals were
noted where usually the woods should have been "alive" with them.

The situation with regard to mice and shrews was not fully realized un-
til the following autumn (1933) when the second attempt to estimate num-
bers by trapping was made.   Then it appeared that the mice had suffered

a decrease of over 80 per cent, and the shrews a decrease of over 65 per cent (Table 15). The reduction in numbers of mice must have reacted directly upon the numbers of shrews, as mice enter so largely into shrew diet.

The summer of 1933 proved to be an especially dry one. The months of June, July, and August were devoid of any effective rainfall (Fig. 5). Such precipitation as did occur came in the shape of more or less violent rainstorms, with rapid run-off of water, and quick drying out of the surface leaves on the forest floor, which afforded no relief to the very dry condition of the humus. The Amphibia, Mollusca, and soft-bodied insects and larvae either perished or went into aestivation. This again meant a shortening of food supplies for the shrews. The mice apparently suffered more than the shrews as indicated by the shift in relative numbers of the two species (Table 15). Not only was their accustomed winter food supply lacking, but the shrews, on shortened rations, due to the disappearance of the insects and other invertebrateas, must have turned to the mice as acceptable food with more persistence than usual.

TABLE 15. Decrease in numbers of mice and shrews.

	1932	1933	1934	1935
Total numbers (5 quadrats):				
Short-tailed shrew.	37	12	6	23
White-footed mouse	28	5	4	27
Relative proportions (percentage of shrews to mice):				
Short-tailed shrew	58	70.6	60	46
White-footed mouse	42	29.4	40	54
Per cent of decrease as compared with 1932:				
Short-tailed shrew	...	67.6	83.8	37.5
White-footed mouse	....	81.4	85.2	4.0

With the short-tailed shrew present in the numbers indicated in the autumn of 1932 (Table 13), one has only to attempt to visualize the enormous amount of animal food necessary for its support to sense the shrew population collapsing under its own weight. This explains the avidity with which baits were taken that autumn; the speedy devouring of so many of the animals trapped; the extension of runways into almost every square foot of ground; the absence in the traps of any other species of shrew. So far as the writer's observation goes, the only real check upon the numbers of shrews in the area was one pair of barred owls and their two young. All barred owl pellets thus far found in the area have, without exception, contained skulls or jaws of *Blarina brevicauda* as well as other material.

If, under optimum conditions, such as apparently existed in 1932, the shrew population got "out of bounds," so to speak, in the absence of sufficiently strong checks, then competition within the species itself would auto-

matically operate to reduce numbers. But as has been indicated, other and even more potent forces were already at work.

Coincident with the increase in the number of rabbits in 1932, there was an increase in the number of foxes hunting in the area, as shown by tracks in the snow in the winter of 1932-33. The number of rabbits was estimated at 40 in January, 1933. On January 15, 1934, with a fine tracking snow on the ground for several days, it was apparent that only 2 rabbits were then inhabiting the area. On the other hand the snow showed the presence of at least 4 hunting foxes—two more than the previous winter. Perhaps the decimation of the numbers of mice and squirrels which may be looked upon as "buffer food," had compelled closer attention to rabbit hunting on the part of the fox population. It is a recognized fact that there always seems to be a perceptible lag in the abundance of the carnivore as related to abundance of food supply (Elton 1927). The record of the snow the following winter (1934-35) showed one fox and no rabbits in the area.

The total disappearance of the skunk following the great reductions in numbers of mice, and the drying out of the humus insects in the summer of 1933 is another significant correlation. So also is the reduction in numbers of the pilot blacksnake.

The yield of beech nuts was again ample in the autumn of 1933 and of 1934, but the sugar maple did not come into bearing again until 1934. The first mammal to show recovery in numbers from the disturbed conditions of 1932 was the chipmunk. There was apparently a small spring brood, and also a summer brood, in 1933; the usual winter activity and a large emerging chipmunk population in the spring of 1934. Apparently numbers were completely recuperated during 1934, and the area seemed to have about all the chipmunks it would normally support. But 1935 proved this assumption wrong, for numbers were again increased. Incidentally this was true not only of the area under study, but chipmunks reached abnormally large numbers throughout the Chagrin valley and elsewhere in the vicinity of Cleveland. The speedy return of the species to normal numbers in the area under study is a notable demonstration of rapid response to favorable conditions in the environment. These must have been close to optimum to have produced such a result.

On the other hand the numbers of shrews and mice continued to drop, so that in the autumn of 1934 trapping records showed a decrease of over 16 per cent for the shrews and almost 4 per cent for the mice as compared with 1933. The shrews were now apparently suffering more than the mice, which would be expected because of the complete restoration of food supplies for the mice but not for the shrews.

The appearance of the pine mouse and the smoky shrew in the traps for the first time (1934), when the numbers of their arch competitor and prob-

able deadly enemy the short-tailed shrew was reduced to a comparatively low figure, seems to indicate that these animals may prosper only when the numbers of the short-tailed shrew are relatively small. Possibly their curve of abundance may fluctuate inversely with that of the short-tailed shrew.

The year 1935 proved to be a "mouse year" at North Chagrin. It witnessed the return of the white-footed mouse to numbers within 4 per cent of the high figures of 1932. The short-tailed shrew showed a substantial increase in numbers over 1934, but was still 37.5 per cent below 1932 numbers. This shift in relative proportions (Table 15) made the white-footed mouse, for the first time during the four years of this study, the most abundant mammal of the area. A new mammal, the pine mouse, appearing first in 1934, became common in the area. As evidence of the pressure of numbers of mice outside the area, the meadow mouse, not normally found in the forest, appears far within the forest boundaries.

Although the foregoing discussion of fluctuations in numbers of mammals is far from complete, yet enough evidence seems to have come to the surface to show how far-reaching a disturbance of the so-called "balance" of nature may be. In this case the disturbance is partly the normal rest in the bearing rhythm of the forest dominants, and partly the abnormal break in the climatic factor of precipitation of moisture. Only in the case of the skunk is there any direct evidence of disease having been a factor in the situation. Competition between individuals and between species seems to have been largely the keen-edged instrument whereby numbers were cut down after the failure of basic food supplies.

THE BIRDS OF THE AREA

As contrasted with the mammals, the birds of the area constitute at times a very rapidly shifting element in the community. From the standpoint of time spent within the area the birds may be divided into the following groups. Scientific names and the order of listing are as given in the American Ornithologists' Union Check List of North American Birds, Fourth Edition, 1931.

TABLE 16. Birds of the area by seasonal groups.

1. Permanent residents

(Species found in the area throughout the year)

Eastern Ruffed Grouse	*Bonasa umbellus umbellus* (Linnaeus).
Northern Barred Owl	*Strix varia varia* Barton.
Northern Pileated Woodpecker	*Ceophloeus pileatus abieticola* Bangs.
Red-bellied Woodpecker	*Centurus carolinus* (Linnaeus).
Eastern Hairy Woodpecker	*Dryobates villosus villosus* (Linnaeus).
Northern Downy Woodpecker	*Dryobates pubescens medianus* (Swainson).
Blacked-capped Chickadee	*Penthestes atricapillus atricapillus* (Linnaeus).
Tufted Titmouse	*Baeolophus bicolor* (Linnaeus).
White-breasted Nuthatch	*Sitta carolinensis carolinensis* Latham.
Eastern Cardinal	*Richmondena cardinalis cardinalis* (Linnaeus).
Red-eyed Towbee	*Pipilo erythrophthalmus erythrophthalmus* (Linnaeus).

2. Autumn and winter visitors

(Species found more or less continuously in the area only in the autumn and winter months)

Northern Blue Jay	*Cyanocitta cristata cristata* (Linnaeus).
Red-breasted Nuthatch	*Sitta canadensis* Linnaeus.
Brown Creeper	*Certhia familiaris americana* Bonaparte.
Winter Wren	*Nannus hiemalis hiemalis* (Vieillot).
Carolina Wren	*Thryothorus ludovicianus ludovicianus* (Latham).
Eastern Golden-crowned Kinglet	*Regulus satrapa satrapa* Lichtenstein.
Eastern Goldfinch	*Spinus tristis tristis* (Linnaeus).
Slate-colored Junco	*Junco hyemalis hyemalis* (Linnaeus).

3. Summer residents

(Species found continuously in the area only during spring and summer)

Northern Crested Flycatcher	*Myiarchus crinitus boreus* Bangs.
Eastern Phoebe	*Sayornis phoebe* (Latham).
Acadian Flycatcher	*Empidonax virescens* (Vieillot).
Eastern Wood Pewee	*Myiochanes virens* (Linnaeus).
Eastern Robin	*Turdus migratorius migratorius* Linnaeus.
Wood Thrush	*Hylocichla mustelina* (Gmelin).
Yellow-throated Vireo	*Vireo flavifrons* Vieillot.
Red-eyed Vireo	*Vireo olivacea* (Linnaeus).
Black-throated Green Warbler	*Dendroica virens* (Gmelin).
Cerulean Warbler	*Dendroica cerulea* (Wilson).
Oven-bird	*Seiurus aurocapillus* (Linnaeus).
Louisiana Water Thrush	*Seiurus motacilla* (Vieillot).
Hooded Warbler	*Wilsonia citrina* (Boddaert).
American Redstart	*Setophaga ruticilla* (Linnaeus).
Scarlet Tanager	*Piranga erythromelas* Vieillot.
Rose-breasted Grosbeak	*Hedymeles ludovicianus* (Linnaeus).

4. Transients

(Species found in the area only during their spring or autumn migration)

Yellow-bellied Sapsucker	*Saphyrapicus varius varius* (Linnaeus).
Yellow-bellied Flycatcher	*Empidonax flaviventris* (Baird and Baird).
Eastern Hermit Thrush	*Hylocichla guttata faxoni* Bangs and Penard.
Olive-backed Thrush	*Hylocichla ustulata swainsoni* (Tschudi).
Gray-cheeked Thrush	*Hylocichla aliciae aliciae* (Baird).
Wilson's Thrush	*Hylocichla fuscescens fuscescens* (Stephens).
Eastern Ruby-crowned Kinglet	*Corythylio calendula calendula* Baird.
Blue-headed Vireo	*Vireo solitarius solitarius* (Wilson).
Black and White Warbler	*Mniotilta varia* (Linnaeus).
Blue-winged Warbler	*Vermivora pinus* (Linnaeus).
Nashville Warbler	*Vermivora ruficapilla ruficapilla* (Wilson).
Magnolia Warbler	*Dendroica magnolia* (Wilson).
Black-throated Blue Warbler	*Dendroica caerulescens caerulescens* (Gmelin).
Myrtle Warbler	*Dendroica coronata* (Linnaeus).
Blackburnian Warbler	*Dendroica fusca* (Müller).
Chestnut-sided Warbler	*Dendroica pennsylvanica* (Linnaeus).
Bay-breasted Warbler	*Dendroica castanea* (Wilson).
Blackpoll Warbler	*Dendroica striata* (Forster).
Connecticut Warbler	*Oporornis agilis* (Wilson).
Canada Warbler	*Wilsonia canadensis* (Linnaeus).
Eastern Purple Finch	*Carpodacus purpureus purpureus* (Gmelin).
White-throated Sparrow	*Zonotrichia albicollis* (Gmelin).
Eastern Fox Sparrow	*Passerella iliaca iliaca* (Merrem).

5. Occasional visitors

(Species noted only occasionally in the area)

Turkey Vulture	*Cathartes aura septentrionalis* Wied.
Sharp-shinned Hawk	*Accipiter velox velox* (Wilson).
Cooper's Hawk	*Accipiter cooperi* (Bonaparte).

Eastern Red-tailed Hawk	*Buteo borealis borealis* (Gmelin).
Broad-winged Hawk	*Buteo platypterus platypterus* (Vieillot).
Eastern Bob-white	*Colinus virginianus virginianus* (Linnaeus).
American Woodcock	*Philohela minor* (Gmelin).
Eastern Mourning Dove	*Zenaidura macroura carolinensis* (Linnaeus).
Yellow-billed Cuckoo	*Coccyzus americanus americanus* (Linnaeus).
Great Horned Owl	*Bubo virginianus virginianus* (Gmelin).
Eastern Whip-poor-will	*Antrostomus vociferus vociferus* (Wilson).
Eastern Nighthawk	*Chordeiles minor minor* (Forster).
Chimney Swift	*Chaetura pelagica* (Linnaeus).
Ruby-throated Hummingbird	*Archilochus colubris* (Linnaeus).
Northern Flicker	*Colaptes auratus luteus* Bangs.
Purple Martin	*Progne subis subis* (Linnaeus).
Eastern Crow	*Corvus brachyrhynchos brachyrhynchos* Brehm.
Starling	*Sturnus vulgaris vulgaris* (Linnaeus).
Bronzed Grackle	*Quiscalus quiscala aeneus* Ridgway.
Eastern Cowbird	*Molothrus ater ater* (Boddaert).
Canadian Pine Grosbeak	*Pinicola enucleator leucura* (Müller).
Eastern Blue Grosbeak	*Guiraca caerulea caerulea* (Linnaeus).
Indigo Bunting	*Passerina cyanea* (Linnaeus).
Common Redpoll	*Acanthis linaria linaria* (Linnaeus).
Red Crossbill	*Loxia curvirostra pusilla* Gloger.

The fact that the blue jay and the Carolina wren are included in the above list as autumn and winter visitors, rather than as permanent residents, may seem strange to one familiar with the birds of the Cleveland region, yet from the standpoint of the forest areas under study this is their status. The record of the blue grosbeak is unusual— a single record of a pair observed by the writer under favorable conditions May 15, 1933, in one of the grape tangles of the area.

DISTRIBUTION AND ABUNDANCE OF BIRDS

Those birds nesting in the beech-hemlock environment only were the black-throated green warbler and probably the ruffed grouse. Those nesting in both beech-maple and beech-hemlock were the wood pewee, wood thrush, and ovenbird. The other species on the lists of permanent and summer residents nested exclusively in the beech-maple association. Most of the transient species were observed in beech-maple environment, while the winter bird companies roamed about the whole area.

The transient species, with the exception of the robins, thrushes, and certain warblers, do not bulk large in numbers. Estimates of 500 robins, 200 thrushes, and 300 warblers have been made at certain times. Autumn and winter visitors are irregularly present except in the case of the slate-colored junco and red-breasted nuthatch. Flocks of from 50 to 60 juncos have been noted, and the red-breasted nuthatch, present in alternate years, sometimes totals 50 to 60 in number.

The permanent resident species became quite well known. The number of hairy and downy woodpeckers, chickadees, tufted titmice, and white-breasted nuthatches are augmented considerably at times during the winter. Whether or not the actual birds nesting in the area in summer are present also in winter is not definitely known. Butts (1930) determined by band-

ing methods that individual chickadees, banded in winter, nested in or quite near their winter feeding territory, and that individual white-breasted nuthatches nested within or very close to their winter feeding area.

The barred owl, the pileated woodpecker, the ruffed grouse, and the cardinal are not usually present in greater numbers in winter than in summer. The towhees congregate in the woods in winter, but in spring most of them leave the area. These probably constitute the towhees nesting just outside the forest, though usually a pair or so may be found nesting just inside the forest edge.

Careful records of the numbers of birds observed on the weekly surveys of the area have been kept over the entire period of this study. The observed occurrence of the bird has been located on a map of the area carried each week for the purpose. Thus the species-constitution, numbers, and territories of the winter bird companies have been determined, the distribution of species and individuals noted, and summer nesting territories charted. While these figures (on their face) reflect seasonal fluctuations, they need considerable interpretation when it comes to studying absolute abundance. Weather conditions influence the count greatly at times. High winds, and storms of snow or rain reduce the number of birds observed. The appearance of the foliage on the forest trees in May is comparable to the dropping of a heavy curtain so far as visibility is concerned. Then sight records are largely replaced by those of hearing. When the song period is over it is quite difficult at times to get evidence of the presence or absence of birds. Chickadees, titmice, nuthatches, and woodpeckers become furtive and inconspicuous at the approach of, and during the nesting season. Differences in weekly counts at times reflect changes in activities or behaviour rather than fluctuations in abundance.

Perhaps the most reliable index to abundance of birds is the record of nesting pairs. By the use of the weekly maps, described above, it is possible to build up a series of maps (one for each species) covering the nesting season, which will show concentrations of records about certain localities. The localities thus indicated may be considered as within the territories of breeding pairs, and it is thus possible to estimate the numbers of breeding pairs of birds throughout the entire area and the approximate extent of the territory occupied by each. Figure 14 is presented as an illustration of this method, the species chosen being the hooded warbler, one of the common nesting species of the area. As nests are actually found, even though it may be during the following winter, their location with reference to the recorded location of the individual birds on the map makes it appear that this method may be relied upon to reveal the presence of a nesting pair or lone male, and fix the approximate limits of the nesting territory.
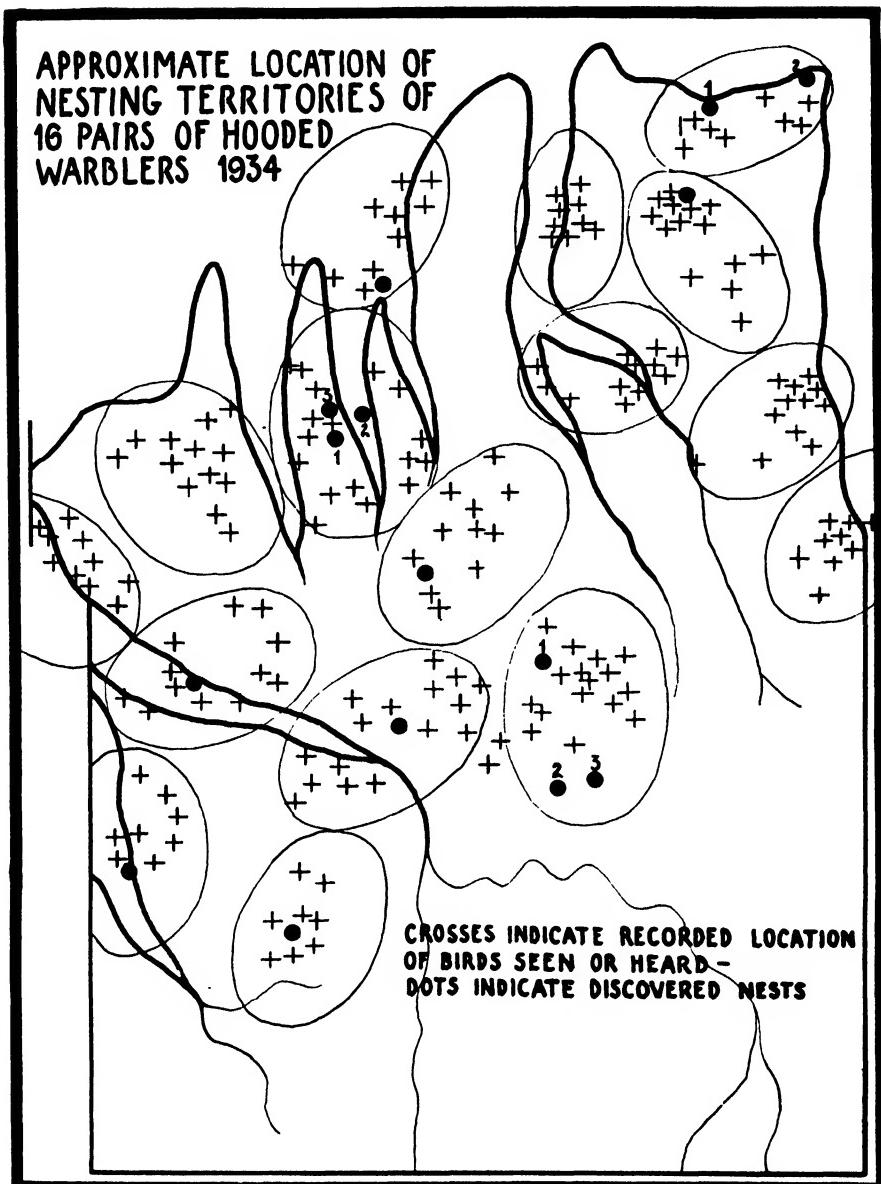
FIG. 14. Approximate nesting territories of hooded warblers in the area under study in 1934, on the basis of records made throughout the nesting season. First, second, and third nests of the same pair are numbered.

Schiermann (1930), studying the density of population of breeding birds in a forest in Brandenburg, Germany, adopted the method of laying out quadrats 250 meters (820.1 feet) square, and then searching systematically for every nest within the quadrat. From these sample quadrats the num-

ber of nesting pairs of birds in the whole area was then estimated. Schiermann found that his statistical results obtained from the quadrat agreed closely with figures arrived at from frequent visits to the area over a period of six years. He concludes, however, that his quadrats are of help only in conjunction with an intimate knowledge of the area obtained from long contact with it. With this conclusion the experience of the writer agrees.

The complete record of nesting birds in the area under study, as determined by the method of charting observed occurrences of the birds on a map, for the summers of 1932, 1933, 1934, and 1935 is shown in Table 17. Second and third attempts at nesting are not counted in this tabulation, but only the number of pairs of birds.

TABLE 17. Numbers of nesting pairs of birds.

Species	Numbers of Pairs			
	1932	1933	1934	1935
1. Red-eyed Vireo	25	36	35	30
2. Wood Thrush	17	25	22	14
3. Hooded Warbler	15	15	16	9
4. American Redstart	12	17	19	19
5. Oven-bird	11	18	16	8
6. Tufted Titmouse	7	8	6	7
7. Black-capped Chickadee	6	5	3	2
8. Eastern Wood Pewee	6	7	7	7
9. Scarlet Tanager	6	6	10	9
10. Eastern Cardinal	5	5	5	4
11. Yellow-throated Vireo	4	4	7	3
12. Acadian Flycatcher	3	3	6	2
13. White-breasted Nuthatch	3	3	4	4
14. Black-throated Green Warbler	3	3	5	3
15. Red-eyed Towhee	3	1	2	1
16. Cerulean Warbler	2	2	1	0
17. Northern Downy Woodpecker	1	4	5	2
18. Eastern Hairy Woodpecker	1	3	3	3
19. Northern Crested Flycatcher	1	2	1	2
20. Eastern Phoebe	1	2	0	1
21. Northern Barred Owl	1	1	1	1
22. Eastern Robin	1	1	1	1
23. Louisiana Water Thrush	1	1	0	1
24. Northern Pileated Woodpecker	1	0	0	0
25. Northern Flicker	0	1	0	0
26. Rose-breasted Grosbeak	0	1	0	1
27. Red-bellied Woodpecker	0	0	1	0
28. Eastern Ruffed Grouse	?	0	0	0
29. Eastern Cowbird	*present*	*present*	*present*	*present*
Total pairs	136	174	176	134
Total individuals	272	348	352	268
Pairs per acre	2.0	2.6	2.7	2.0
Pairs per hectare	4.9	6.4	6.7	4.9
Average number pairs per acre, 4 years				2.3
Average number pairs per hectare, 4 years				5.7

It will be noted that the summer of 1933 showed a slight increase in numbers of nesting pairs, as contrasted with the great decrease in the mammal population of this period. The birds were unaffected by the failure of beech and sugar maple seeds, as these are not "basic" foods for them, as they are in the case of most of the mammals. They were also not affected by the dry weather of the summer so far as nesting activities were concerned, as the drought was most severe during late June. July, and August, when nesting activities were about over. If the bird population was affected by reduced numbers of insects following the drought, or if reproduction was cut down during the breeding season one would expect it to be reflected in the numbers of breeding pairs in 1934.

Figure 15 shows the approximate locations of the nesting sites of the 176 pairs of birds listed in Table 17 as having been recorded in 1934. As this figure is studied it should be kept in mind that we have here not only a horizontal distribution of nesting sites, but a vertical one as well, ranging from the tops of large trees, as in the case of the cerulean warbler, down through the various levels of forest growth to the nesting site of the oven-bird beneath the leaf-litter on the floor of the forest. Nesting territories may be separated from each other by distance vertically as well as by distance horizontally. The writer recalls one nest of the red-eyed vireo approximately 70 feet (21.3 meters) up, in a large beech tree, and another nest of the same species almost directly below it in a beech sapling about 6 feet (1.8 meters) from the ground. One vireo pair had a tree-top territory, the other almost a ground-level territory.

Using the breeding record as a basis for estimating the summer breeding population of birds, and the weekly counts of numbers observed at all seasons of the year, with due allowance for weather and other conditions affecting the counts, Table 18 has been prepared as an attempt to estimate the total bird population present at various times throughout the year. Only the fairly well-known species are included in this list as such. Others are totaled under appropriate headings. Young birds are not counted until they become independent of parents. While the figures are an attempt to approximate the highest population numbers reached each month even this figure is of course not constant during the month.

FOOD CHAINS AND ECOLOGICAL NICHES

While the numbers of nesting pairs of birds in the area may at first glance seem to crowd the territory unduly, yet competition for food is really limited by reason of the territorial relations of competing species or individuals, and the particular ecological niches in the forest community occupied by others.

The barred owl, the ruffed grouse, and the robin probably do not com-
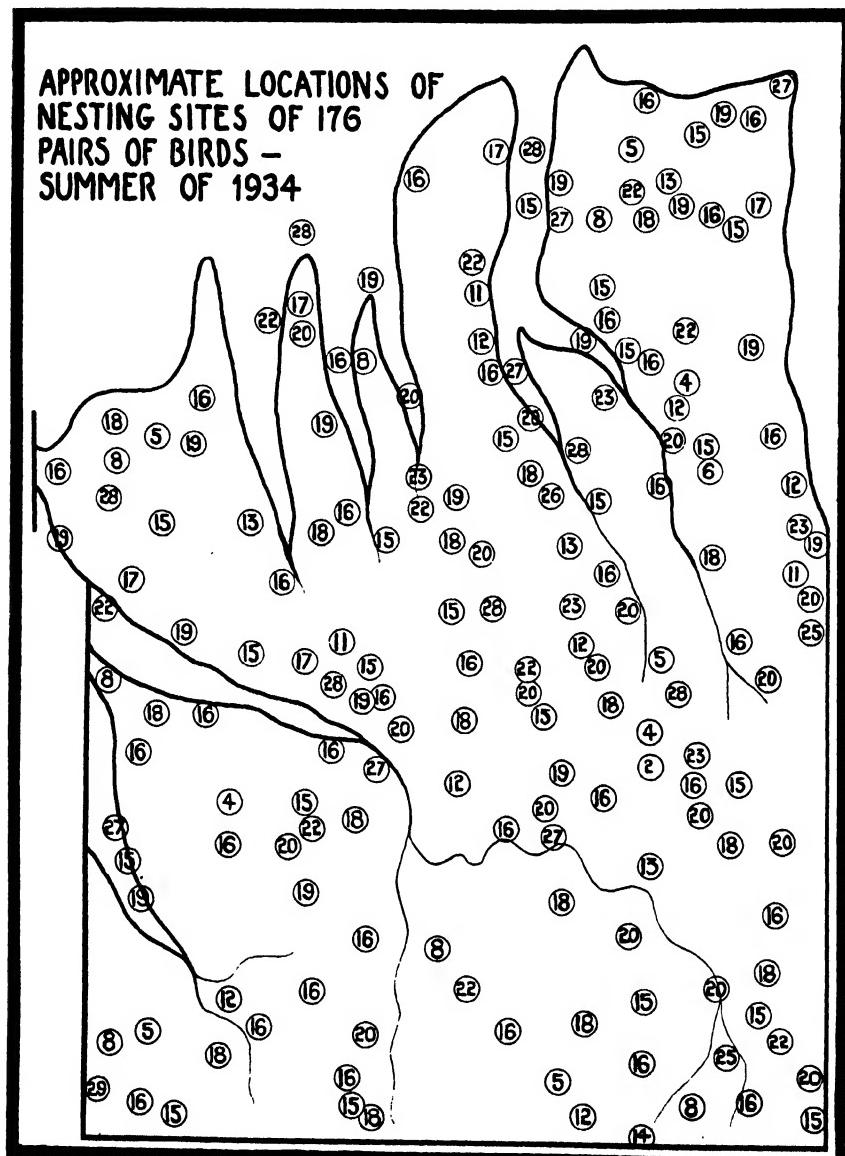
FIG. 15. Approximate locations of nesting sites of breeding birds in Table 17, summer of 1934.

2—Barred owl
4—Hairy woodpecker
5—Downy woodpecker
6—Crested flycatcher
8—Wood pewee
11—Chickadee
12—Tufted titmouse
13—White-breasted nuthatch

14—Robin
15—Wood thrush
16—Red-eyed vireo
17—Black-throated green
       warbler
18—Oven-bird
19—Hooded warbler

20—Redstart
22—Scarlet tanager
23—Cardinal
25—Towhee
26—Cerulean warbler
27—Acadian flycatcher
28—Yellow-throated vireo
29—Red-bellied woodpecker

TABLE 18. Estimated average bird population by months based on 1932, 1933, 1934, and 1935 figures.

	March	April	May	June	July	August	September	October	November	December	January	February
Permanent residents:												
Tufted Titmouse	20	20	14	14	12	12	12	20	20	20	20	20
Eastern Cardinal	10	10	10	10	10	10	10	10	10	10	10	10
White-breasted Nuthatch	16	16	10	6	6	6	12	12	30	20	16	16
Black-capped Chickadee	16	16	8	8	8	8	16	16	16	16	16	16
Northern Downy Woodpecker	16	16	8	6	6	6	10	10	16	16	16	16
Eastern Hairy Woodpecker	6	4	4	4	4	4	8	8	8	8	6	6
Red-eyed Towhee	10	10	10	4	4	4	4	4	10	10	10	10
Northern Barred Owl	2	2	2	2	2	2	2	2	2	2	2	2
Northern Pileated Woodpecker	2	2	2	0	0	0	2	2	2	2	2	2
Red-bellied Woodpecker	1	1	0	0	0	0	1	1	1	1	1	1
Eastern Ruffed Grouse	1	1	1	0	0	0	0	1	1	1	1	1
Totals	100	98	69	54	52	52	78	86	116	106	102	100
Summer residents:												
Red-eyed Vireo			82	62	50	30	20					
Wood Thrush			54	38	32	20	10	2				
American Redstart			50	34	16	8						
Hooded Warbler			28	28	20	14	10	1				
Oven-bird			40	26	14	8	6	5				
Scarlet Tanager			16	16	12	8	4					
Eastern Wood Pewee			10	14	14	10	6					
Yellow-throated Vireo			10	8	6	2	2					
Acadian Flycatcher			6	6	4	4	4					
Black-throated Green Warbler		10	25	6	6	2	30	2				
Eastern Cowbird		2	4	6								
Cerulean Warbler			20	2	2	2	2					
Northern Crested Flycatcher			4	2	2	2	1					
Louisiana Water Thrush		4	10	2	2	2						
Eastern Phoebe			4	2	2	2						
Eastern Robin		6	2	2	2	10	100	500	250	2	2	2
Totals		22	365	254	184	124	195	510	250	2	2	2
Autumn and winter visitors, transients and occasionals												
Autumn and winter visitors	20	30	10				25	75	50	30	10	10
Red-breasted Nuthatch	20	40	15				10	60	75	50	30	25
Slate-colored Junco	50	50						50	50	25	10	5
Transient Warblers		10	300			15	150	50				
Eastern Hermit Thrush		30						50				
Olive-backed Thrush			75				50	75				
Gray-cheeked Thrush			10				10					
Wilson's Thrush			25				10	15				
White-throated and Fox Sparrows		20	50				10	75	10			
Occasional visitors	15	20	20	5	5	20	30	15	10	5		15
Totals	105	200	505	5	5	35	295	465	196	110	50	55
Grand Total	205	320	939	313	241	211	568	1061	562	218	154	157

pete with any other species for food. The woodpeckers, while all seeking their food in the same way, probably overlap very little, as the different species work upon different parts of the larger trees, and the downy pays a

good deal of attention to lesser growth, not worked by the other larger birds. While the 3 pairs of white-breasted nuthatches may sometimes come into competition with the downy woodpeckers, their nesting sites are widely separated so that competition is reduced to a minimum. The nuthatches may come into real competition with the chickadees and titmice, but this combination represents but 18 pairs of birds at its recorded maximum during the nesting season, which allows 3.6 acres (1.45 hectares) to the pair if the territory were evenly divided between them. As a matter of fact the chickadee and titmouse nesting territories seem to be complementary to each other, while the nuthatches cover a much wider range than either of the others.

So far as food habits are concerned the flycatchers form a group by themselves, each species having its own special hunting ground. The crested flycatcher pairs keep strictly to its part of the woods. The Acadians each have their own little glen, with a stream running through it, and no other flycatchers in the vicinity. The wood pewees have widely separated territories of their own in the higher levels of the forest. The hooded warblers and the redstarts may compete at times with each other, yet in a general way they are somewhat complementary as the redstart usually hunts in higher territory than does the hooded warbler.

The birds whose food habits call them frequently or almost entirely to the ground in summer—the Louisiana water thrush, oven-bird, wood thrush, cardinal, towhee—have about 2 acres (0.8 hectares) per pair on the average, which would furnish them with plenty of food supplies not drawn upon to any extent by other species.

This reserves the leafy foliage of the forest trees to the tanagers, vireos, and cerulean warblers—not entirely, of course, but this is their particular niche. The black-throated green warblers seem to keep pretty closely to the upper parts of the large hemlock trees during the nesting season, and their nesting sites are widely separated.

So far as factors within the environment are concerned this summer population of breeding birds seems to be regulated largely in its distribution and density within the area by the available food supplies, and the number and fitness of nesting sites and ecological niches offered by the forest environment.

It is difficult, if not impossible, to assign places of relative influence to particular species of birds inhabiting the community. In the aggregate the birds consume an immense amount of insect food as well as considerable vegetable matter. Certain groups, however, may be singled out as of outstanding importance because of numbers, or because of their constant activity throughout the year.

Probably the most influential of these groups is that composed of the

hairy and downy woodpeckers, chickadee, tufted titmouse, and white-breasted nuthatch.   These are all permanent resident species, and their numbers are considerably increased at certain times of the year.   They constitute a company of very diligent searchers after insects on and under the bark of trees, and in dead wood, dividing between them the territory to be covered, so that very little tree surface escapes their attention.   Larvae of beetles and other insects, eggs, pupating insects, hibernating insects, spiders, myriapods, and others form the bulk of their diet.   Beech nuts are eaten by all of these species as well as many wild fruits.   Their limited range keeps them within the area, and thus entirely dependent upon it for their food supplies.

There is no doubt but that the heaviest summer influence is exercised by the group composed of wood thrush, oven-bird, hooded warbler, red-eyed vireo, redstart, and scarlet tanager.   All these are highly insectivorous. They cover all levels from ground to tree-tops, and so serve as an efficient check to the summer insect population.   Yet their stay in the area is limited, and their activities are spread over too short a space of time to give them first rank in influence.   They supplement the activities of the first group when the insect tide is rising to its greatest proportions, and it may be questioned whether, in the absence of either group the forest could long continue to maintain itself.   It is of interest to note how, in August, the chimney swifts and purple martins, hunting immediately above the forest roof, complete the occupation of all levels in the community of forest animals.

Another great bird group is that composed of robins, hermit thrushes, and olive-backed thrushes in autumn.   Although these birds come mainly for forest fruits, among which the wild grape ranks high, they also spend much time raking over the dead leaves of the forest floor for insect food. Of great importance also is the frequently large group of migrating warblers in spring.   Though their stay in the area is brief, they rid the developing foliage and bark surfaces of the trees of many newly hatched insects before the minuate larvae have developed into larger consumers of foliage.

The most important non-breeding bird in the area is the red-breasted nuthatch.   Though present only in alternate winters during the period of this study, and though their numbers are marked by considerable fluctuation, they often surpass in numbers all other species put together.   Their length of stay covers a period of over seven months, and while present they are apparently strictly resident.   They are very diligent in their pursuit of food, spending much time searching the bark, limbs, twigs, and decayed places of the forest trees.   Beech nuts are taken with evident relish.   The red-breasts work all the way from the ground to the tops of the highest trees, and do not hesitate to enter the cavities of decaying logs.

The barred owl and the pileated woodpecker stand out because of their size and year-round activity.   The woodpecker's range is much larger

than the area under study, and though a single pair, sometimes augmented
by young in summer, or another presumably immature bird in winter,
spend much time in the area, they are not dependent upon it for their liv-
ing. Their work on hemlock trees infested by the bark-boring beetle is
very evident. They also do much work in digging for grubs and ants in
trees like the white ash, in which the heart-wood is decayed, but the sap-
wood is still sound. The pileated woodpecker is an influential bird in the
area, but important in a supplementary way rather than primarily. On the
other hand, the barred owl is more nearly resident, probably not going far
beyond the limits of the area on his hunting trips. In summer the single
pair of owls breeding in the beech-maple association seem to hold them-
selves and their young quite closely to the interior forest, appearing to be
entirely dependent upon it for food supplies.

That short-tailed shrews form the bulk of the owl's diet is very appar-
ent. The barred owl has frequently been observed in the act of catching
these little animals, and no cast pellet so far examined has failed to include
jaws or skulls of from 1 to 4 shrews (*Blarina brevicauda*). Remains of the
white-footed mouse are also frequently found, but not always, as is the case
with the shrew. Though these two animals probably make up most of the
barred owl's diet, the writer is inclined to the opinion that a considerable
number of the smaller insectivorous birds are also consumed, especially in
early spring when the summer resident bird population is concentrating its
activities upon the incubation of eggs and rearing of young. The frequently
deserted and destroyed nests found at this season strongly suggest that the
incubating or brooding bird has come within range of the owl's telescopic
vision, and has been picked off—sometimes nest and all. When the owl's
nesting site was examined in April 1932, after the young had come off,
feathers of hairy woodpecker, red-bellied woodpecker, blue jay, cedar wax-
wing (*Bombycilla cedrorum* Vieillot), bob-white, and horned lark (*Otocoris
alpestris* Linn.) were recovered from the débris at the bottom of the nesting
cavity. The presence of horned lark feathers certainly indicates an ex-
cursion into the open fields outside the woods, and the bob-white and cedar
waxwing remains are corroborative evidence of the same thing. The barred
owl therefore is of large importance in the community as a check upon the
numbers of shrews and mice, and to a much less extent as a limiting in-
fluence on the reproduction of smaller birds within the area.

It is more difficult to classify the birds of the area on the basis of food
habits than it is the mammals. The barred owl is the only one among the
permanent residents to be classed as a carnivore. Yet he is also an eater
of insects (Fisher 1880). The other permanent residents, while all con-
suming considerable vegetable matter, particularly beech nuts, could prob-
ably, with the possible exception of the ruffed grouse, get along quite well in

the absence of vegetable provender. The summer residents are predominantly insectivorous—the flycatchers, warblers, vireos, and tanager completely so (Forbush 1927, 1929). Thus it appears that the bird population of the area, with the exception of the barred owl, is supported mainly by the insect food supplies of the forest, and only secondarily, and to a much less extent, by plant products.

SEASONAL CHANGES IN THE BIRD POPULATION OF THE AREA

One of the main characteristics of the bird population of the area under study is its instability. Fluctuations in numbers are at times extreme, and even in winter numbers are far from constant. While the total of species listed is 83 (Table 16), only 11 of these are classed as permanent residents. Even the summer nesting species constitute a rapidly shifting element in the total bird population. What the increase in numbers may be when young birds are launched upon independent careers is largely a matter of conjecture, for it is certain that most of the summer resident species leave the area with their young as soon as the latter are capable of sustained flight. One must also allow for a large mortality among both young and old, and must count upon a large percentage of failures of nesting pairs to bring any young birds off the nest. Butts (1930), working with banded white-breasted nuthatches, noted the frequent disappearance of apparently permanent resident birds. Out of 21 individuals, 10 disappeared in two years, and only one, banded at the beginning of his study, lasted throughout the three years of its duration. Probably the length of life of most small birds is not more than two years on the average. The probability is that when the summer is over, the net increase in the bird population is not large. Depletions from the ranks of the older birds are made good by the entrance of younger birds into the community, perhaps in numbers just large enough to absorb the losses that are due to come as a result of autumn and winter casualties, and so maintain the species at about its normal numbers.

Reference to Table 18 will give an idea of constantly changing numbers, but when this is reduced to diagrammatic form (Fig. 16) the often extreme and abrupt fluctuations as well as the more gradual changes in the bird population of the area are clearly apparent. As the red-breasted nuthatch has been present only on alternate years, this species is set off from the other winter visitors.

It is in the spring and autumn that the fluctuations in number of birds in the area are relatively enormous. During the first half of the month of May the woods are flooded with migrant species on their way to more northerly breeding grounds. At the same time the greater number of the summer resident species are arriving. In October and November the woods are again filled with large numbers of robins and flocks of migrating thrushes
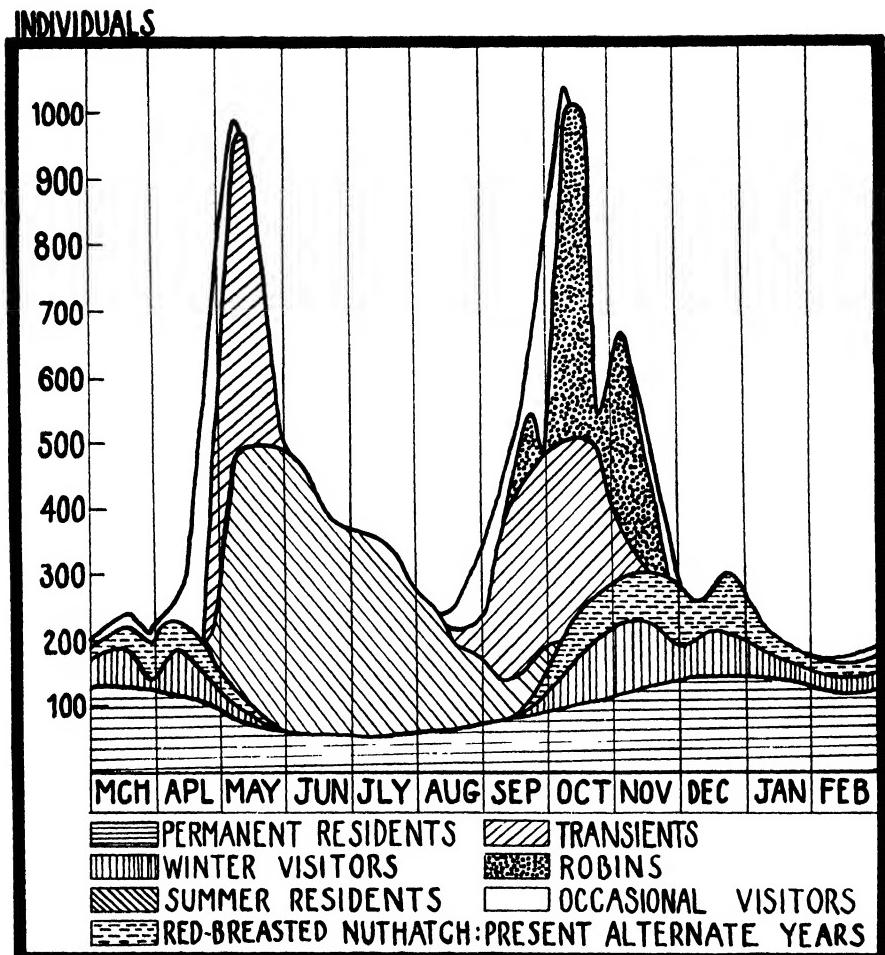
FIG. 16. Seasonal fluctuations in the bird population of the area under study on the basis of estimates and averages of weekly counts for 1932, 1933, and 1934.

and sparrows. The winter visitors are already well massed in October and reach a peak of numbers in November. These two months witness the largest assemblage of birds in the area during the year. The two periods of least numbers are the second week in August, when the summer population is depleted, and the last week in January, when many of the winter visitors have left the area and the influence of the northward movement is so soon to come is not yet evident.

THE REPTILES OF THE AREA

During the first two and a half years of this study the only reptiles observed in the area were snakes. In the spring of 1934 Mr. M. B. Walters

and the writer together were fortunate enough to get very good sight records of several five-lined skinks, thus adding a lizard to the list. The reptiles thus far observed, specimens of all of which except the skink have been collected, are shown in Table 19. Scientific names are as used by Ditmars (1920).

TABLE 19. Reptiles of the area.

Five-lined Skink	*Eumeces quinquelineatus* (Linn.).
Ribbon Snake	*Eutaenia saurita* (Linn.).
Common Garter Snake	*Eutaenia sirtalis* (Linn.).
Common Water Snake	*Tropidonotus fasciatus sipedon* (Linn.).
De Kay's Snake	*Storeria dekayi* (Holbrook).
Red-bellied Snake	*Storeria occipitomaculata* (Storer).
Pilot Blacksnake	*Coluber obsoletus* (Say).
Milk Snake	*Ophibolus doliatus triangulus* (Daudin).

The skinks were observed on May 7, 1934, running in and out from under the loose bark on a large fallen beech log, evidently enjoying the brilliant spring sunshine which was a feature of that day. Three were seen at one time and two at another, but the total number may not have been more than three. One of these was in the "blue-tailed" stage, the others brown, with characteristic red heads. As this is the only recorded occurrence of these animals in the area their numbers must be few.

The common garter snake and the ribbon snake, while regularly found, are not abundant. Five small immature common water snakes have been taken in or near the course of the main stream bed in the area. This species is common in a pond about a half mile west of the area, and these young snakes may possibly have come into the woods from that direction. Three specimens only of the milk snake have been taken. Five fine examples of the red-bellied snake have been found, one of which, while in temporary captivity, gave birth to 21 living young. The period of activity of these snakes is from about May 1 to the latter part of October.

The only reptile inhabiting the area that can be said to be present in numbers is the pilot blacksnake. During the summer of 1931 12 or 13 of these beautiful serpents were taken in the area. Most of these were over 4 feet (121.9 cm.) in length; several were over 5 feet (152.4 cm.); and the cast "skin" of one has been found measuring 6 feet 1 inch (185.3 cm).

After several days in captivity the pilot blacksnake can be handled easily. Captive specimens have proved to be remarkably expert in climbing, and exceedingly muscular in action. According to Ditmars (1920), the snakes of the genus *Coluber*, to which the pilot blacksnake belongs, feed upon warm-blooded prey exclusively—especially the smaller rodents—and also upon birds and their eggs. One is mentioned as having disgorged a well-grown cottontail rabbit upon being captured. Captive snakes of this species, observed by the writer, took three young scarlet tanagers which were found dead, their nest having been blown down in a storm. One was reported as

having been seen coiled about a wood thrush's nest some 20 feet (6 meters) above the ground in a young sugar maple sapling, having apparently made a meal of the young birds.

When released, these snakes quickly disappear beneath the leaf litter, or into any near-by cavity under a log or stump. One can easily see what an efficient hunter of chipmunks, mice, shrews, and young birds an animal of this sort might be.

The earliest record of the appearance of the pilot blacksnake in spring in the area is May 2. On this date the writer saw a fine specimen which when measured later proved to be 4.5 feet (137.1 cm.) in length. There was considerable soil adhering to the reptile's back, as though he might have just emerged from an underground retreat. He was lethargic, allowing the camera tripod to be set up within a few inches of his head, and when picked up showed no signs of fight, which is unusual in this species. The inference was that he had just emerged from hibernation. As these snakes disappear in October, this allows for a full six months period of activity.

As to the rate of reproduction of the pilot blacksnake, one captive specimen, 5 feet 4 inches (162.5 cm.) long deposited 22 eggs on July 18. Several days later, another of lesser length laid 13 eggs.

The pilot blacksnake is well distributed throughout the area, having been observed in all parts of it, including beech-hemlock environment. During the past three years 10 of these snakes have been marked by making a deep V-shaped nick in the outer edge of one of the ventral plates, and then have been set at liberty. The number of the marked plate, counting from the anus has been recorded in each case, being a different number for each snake. One of these, marked in the summer of 1932, was recovered near the point of original capture and set at liberty again May 6, 1934. This would seem to indicate a rather closely resident character for these serpents. The numbers of pilot blacksnakes, judging from captures made, seemed to be fairly constant in 1932 and 1933, but were distinctly less in 1934 and 1935. This is apparently correlated with the falling off in numbers of small mammals in 1933 and 1934.

The importance of the garter snake, ribbon snake, and water snake in the area seems relatively very small because of their insignificant numbers, small size, and food habits which restrict them to insects, worms, frogs, and toads. If the milk snake should be found here in numbers, it would need to be classed as an important member of the community, but at present there is no evidence that this is the case. The red-bellied and De Kay's snakes may be present in greater numbers than the few records indicate. They are secretive in habits, and normally not often seen. Ditmars (1920) says that the food of these snakes consists of earthworms, slugs, and the soft-bodied grubs of beetles. Their burrowing habits might make them

important insect hunters in decaying stubs and logs. If present in numbers they would therefore be important members of the forest community.

The pilot blacksnake must be classed as among the really important members of the community. In size, in numbers, in food habits, in rate of reproduction, and in activity it ranks well up among the more important animals of the area.

THE AMPHIBIA OF THE AREA

The list of amphibians thus far discovered in the area is shown in Table 20.

TABLE 20. Amphibia of the area.

Toads and frogs

American Toad	*Bufo americanus* Le Conte.
Fowler's Toad	*Bufo fowleri* Putnam.
Pickering's Hyla	*Hyla crucifer* Wied.
Green Frog	*Rana clamitans* Latreille.
Eastern Wood Frog	*Rana sylvatica* Le Conte.

Salamanders

Brown Salamander	*Desmognathus ochrophaea* Cope.
Dusky Salamander	*Desmognathus fusca* (Rafinesque).
Spotted Salamander	*Ambystoma punctatum* (Linn.).
Mole Salamander	*Ambystoma talpoideum* (Holbrook).
Red-backed Salamander	*Plethodon cinereus* (Green).
Slimy Salamander	*Plethodon glutinosus* (Green).
Red Eft	*Triturus viridescens* Rafinesque.

Toads and frogs are not abundant in this forest community. But 3 records of the American toad, and 5 of Fowler's toad have been made. The wood frog and Pickering's hyla occur more frequently but have never been observed in numbers. Each is generally distributed throughout the area, but more often encountered on the lower levels than on the higher land. During the summers of 1931 and 1932 the green frog was the common frog of the area. Nearly every pool of standing water had its one or more small half-grown frog of this species. During dry weather they would disappear, but after a rain would appear again. In 1933 green frogs were scarce in the area, and in 1934 and 1935 they were completely absent. After the dry summer of 1933 all frogs became exceedingly scarce in the area.

Nor are salamanders abundant. The commonest species is *Triturus viridescens* in the second larval form commonly known as the "red eft." The adult form is very common in a pond to the west of the area. After a rain in summer these brilliant red salamanders may be seen walking abroad quite fearlessly. The writer has seen both the raccoon and the crow refuse to eat the red eft, though they would take salamanders of other species. Perhaps this matter of being unpalatable may account for the somewhat greater abundance and lack of fear of this species. The dusky salamander is quite abundant in certain wet places under stones in stream beds. The red-backed and brown salamanders are both found sparingly under logs and bark or in moist dead wood. The slimy salamander seems to be

rather generally distributed through both associations, but quite sparingly, while the spotted salamander and the mole salamander are rare. After the very dry summer of 1933 all salamanders became quite rare in the area, the red eft being the only species that seems to have escaped a drastic reduction in numbers.

Not much can be said at this time as to the relative importance of amphibia in the area. That frogs are an item in the fare of the raccoon may be infered from the abundance of the raccoon tracks about the places where frogs are to be found. Doubtless most of the other amphibians, when encountered, would be added to the raccoon's diet. The same would hold true for the skunk and the opossum, and doubtless for other mammals and some birds. The ribbon snake, the garter snake, and the water snake are known to be addicted to amphibian fare (Ditmars 1920).

On the other hand the toads, frogs, and salamanders fill a definite niche in the economy of the forest as large consumers of insects, slugs, and larvae. Yet because of their small numbers in the area under study they do not seem to be of great importance to the community as a whole.

INVERTEBRATES OF THE AREA

The molluscs listed in Table 21 have all been collected as live animals within the area and the dead shells of many of them are quite common on chipmunk feeding tables and in shrew runways.

TABLE 21. Molluscs of the area.

Polygyra stenotrema (Ferussac).	*Polygyra fraterna* (Say).
Polygyra tridentata (Say).	*Omphalina inornata* (Say).
Polygyra fraudulenta (Pilsb.).	*Omphalina fuliginosa* (Griffith)
Polygyra albolabris (Say).	*Anguispira alternata* (Say).
Polygyra albolabris dentata Tyron.	*Succinea retusa* Lea.
Polygyra thyroides (Say).	*Succinea ovalis* Say.
Polygyra clausa (Say).	*Circinaria concava* (Say).
Polygyra zaleta (Binney).	*Vitrea hammonis* (Ström.)
Polygyra palliata (Say).	*Zonitoides minuscula* (Binney).
Polygyra hirsuta (Say).	*Limax maximus* Linnaeus.

Cahn and Kemp (1929) mention finding the shells of *Anguispira alternata* and *Polygyra stenotrema* in nests of the white-footed mouse. Shull (1907) found that in winter, snails of the genus *Polygyra (albolabris, multilineata, profunda, thyroides, fraterna)* formed much of the food supply of the short-tailed shrew. That land snails are preyed upon by certain beetles and their larvae is also established (Lengerken 1934, Boettger 1934). Boycott (1934) says that competition between land snails is an almost negligible factor, and that there is no specific relation between Mollusca and trees.

The crayfish *Cambarus bartoni robustus* Girard is common in the main stream bed of the area. Crayfish are said to be fed upon by raccoons, salamanders, frogs, birds, snakes, turtles, and fishes (Turner 1926). The same

author says that crayfish are generally omnivorous, eating almost anything of an organic nature that comes to hand, whether of animal or vegetable material.

The temporary pools in the beech-maple association were studied in the spring of 1933 by Dr. Norma C. Furtos. During this study the temperature of the water varied from 40° C. (39.2° F.) on April 8 to 15° C. (59.° F.) on April 28. Organisms found are listed in Table 22.

TABLE 22. Organisms in temporary pools.

Arcella sp.	*Candona decora* Furtos.
Trachelomonas sp.	*Candona brevis* Muller.
	Eucypris sp.
Planaria velata Stringer. (common)	*Eucypris fuscata* (Jurine) var.
	gigantea Furtos.
Alona guttata.	*Eucypris* sp.
Chydorus sphaericus (O. P. Müller).	*Cypricercus tincta* Furtos.
Cyclops viridis Jurine.	*Cryptocandona* sp.
Cyclops crassicaudis Sars.	
Cyclops serrulatus Fischer.	*Gammarus* sp.
Cyclops bicuspidatus Claus.	*Eucrangonyx* Sp.
Canthocamptus staphylinoides (Jurine).	*Macrobiotus* sp.

In addition to the species listed (Table 22) aquatic earthworms were commonly found, a small crayfish was taken, and larvae of caddis fly, may-fly, *Diptera* and *Coleoptera*, were found to be common. Mosquito larvae were very abundant. Red water mites were common.

Obviously no complete understanding of the dynamics of the forest can be secured without a thorough study of its insect life. This should be done quantitatively as well as qualitatively. On all sides the evidences of the activities of wood-boring and bark-boring insects are apparent. There are bees and flies and wasps and butterflies and small midges and mosquitoes in the air. Moths large and small are common. The big syrphid fly *Milesia virginiensis* Dru. is common, as are the scavenger beetles *Necrophorus marginatus* Fab. Camel crickets are abundant in the humus in certain places. Ground beetles are abundant everywhere. The yellow-jacket *Vespa communis* De S. and the white-faced hornet *Vespula maculata* (Linn.) are very common. The writer counted 9 large nests of the latter species in the winter of 1934-35 in the area. The work of the flat-headed hemlock borer *Melanophila fulvoguttata* Harr. is very noticeable in the beech-hemlock areas. The fungi of the area support a numerous insect population. In September the white woolly aphid *Schizoneura imbricator* Fitch. is often noted on the branches of the beech. Various kinds of caterpillers are noted on the foliage of the trees, and vireos and warblers seem to find much to glean from foliage beyond the range of one's vision. In August and September the hum of insects is a definite feature of the forest.

By reason of their numbers, their destructive activities from the standpoint of plant life, their rôle as reducing agents in dead and decaying tim-

ber, their interrelations within their own group, their relations to other
animals as parasites, and their great importance as a source of food supply,
insects occupy a place of great significance in the biotic community. While
their importance is recognized, it is impossible here to do more than call at-
tention to it.

ECOLOGICAL CLASSIFICATION OF ANIMALS

The study of animal ecology has not as yet developed a commonly ac-
cepted terminology. As that suggested by Smith (1928) does not seem to
the writer to be entirely adequate to some of the situations arising in this
study, the following special terms are herein employed:

1. Predominants are those animals which are most abundant in num-
bers and of greatest influence in the community.

2. Members are those animals that are present in smaller numbers than
predominants, and therefore of lesser influence. The term may be applied
to a single individual.

Both predominants and members may be further subdivided by employing
the following adjectives.

1. Permanent. Used to indicate constant presence and activity through-
out the year.

2. Fluctuating. Used to indicate marked lack of constancy in numbers
and activity at different seasons, although present throughout the year.

3. Seasonal. Used to indicate presence or activity at one or more
seasons of the year and entire absence or inactivity at others.

4. Incidental. Used to indicate irregular and inconsequential occur-
rence in the community.

TABLE 23. Ecological classification of vertebrates in the beech-maple association.

Predominants	Members
Permanent predominants	Permanent members
Mammals	Mammals
Short-tailed Shrew	Eastern Red Fox
Northern White-footed Mouse	New York Weasel
	Southern Red Squirrel
	Small Eastern Flying Squirrel
	Domestic Dog
	Domestic Cat
Birds	Birds
Eastern Hairy Woodpecker	Eastern Ruffed Grouse
Northern Downy Woodpecker	Northern Barred Owl
Black-capped Chickadee	Northern Pileated Woodpecker
Tufted Titmouse	Red-bellied Woodpecker
White-breasted Nuthatch	Eastern Cardinal
Fluctuating predominants	Fluctuating members
Mammals	Mammals
Northern Gray Squirrel	Cottontail Rabbit
Eastern Chipmunk	Smoky Shrew
Pine Mouse	
Birds	Birds
Eastern Robin	none

Seasonal predominants		**Seasonal members**
Mammals		Mammals
none		Virginia Opossum
		Eastern Raccoon
		Eastern Skunk
		Southern Woodchuck
		Big Brown Bat

Seasonal predominants
  Mammals
    none

  Birds
   (nesting species
   Red-eyed Vireo
   Wood Thrush
   Hooded Warbler
   American Redstart
   Oven-bird
   Eastern Wood Pewee
   Scarlet Tanager

   (transient species)
   Eastern Hermit Thrush
   Olive-backed Thrush

   (winter resident species)
   Red-breasted Nuthatch
  Reptiles
   Pilot Blacksnake

  Amphibians
   Green Frog
   Wood Frog
   Pickering's Hyla

  Red Eft
  Red-backed Salamander

Seasonal members
  Mammals
   Virginia Opossum
   Eastern Raccoon
   Eastern Skunk
   Southern Woodchuck
   Big Brown Bat

  Birds
   (nesting species)
   Crested Flycaster
   Acadian Flycaster   K
   Eastern Phoebe
   Yellow-throated Vireo
   Cerulean Warbler
   Louisiana Water Thrush
   Rose-breasted Grosbeak
   Red-eyed Towhee

   (transient series)
   American Woodcock
   Yellow-bellied Flycatcher
   Winter Wren
   Gray-cheeked Thrush
   Wilson's Thrush
   Eastern Golden-crowned Kinglet
   Eastern Ruby-crowned Kinglet
   Blue-headed Vireo
   Black and White Warbler
   Blue-winged Warbler
   Nashville Warbler
   Magnolia Warbler
   Black-throated Blue Warbler
   Blackburnian Warbler
   Chestnut-sided Warbler
   Blackpoll Warbler
   Connecticut Warbler
   Canada Warbler
   Purple Finch
   White-throated Sparrow
   Fox Sparrow
   Yellow-bellied Sapsucker
   (winter resident species)
   Eastern Goldfinch
  Reptiles
   Five-lined Skink
   Ribbon Snake
   Garter Snake
   Red-bellied Snake
   De Kay's Snake
   Milk Snake

  Amphibians
   American Toad
   Fowler's Toad

   Dusky Salamander
   Brown Salamander
   Slimy Salamander

Incidental Members
Mammals

Fox Squirrel	Hairy-tailed Mole
Meadow Mouse	Red Bat
Star-nosed Mole	Silver-haired Bat

Birds

Turkey Vulture	Chimney Swift	Eastern Blue Grosbeak
Sharp-shinned Hawk	Ruby-throated Hummingbird	Indigo Bunting
Cooper's Hawk	Northern Flicker	Common Redpoll
Eastern Red-tailed Hawk	Northern Blue Jay	Red Crossbill
Broad-winged Hawk	Purple Martin	Slate-colored Junco
Eastern Bob-white	Eastern Crow	Eastern Whip-poor-will
Eastern Mourning Dove	Starling	Reptiles
Yellow-billed Cuckoo	Brown Creeper	Common Water Snake
Great Horned Owl	Carolina Wren	Amphibians
Eastern House Wren	Bronzed Grackle	Spotted Salamander
Eastern Nighthawk	Eastern Cowbird	Mole Salamander

ASPECTION

Aspection, or phenology, has to do with the visible evidence of the responses which plants and animals make to the changing of the seasons. It is usual to divide the year on the basis of plant activity into six main periods, or aspects; the prevernal, vernal, aestival, serotinal, autumnal, and hibernal (McDougall 1927, Weaver and Clements 1929). While this has been adopted also for animals as a convenient way of designating seasonal changes, it is difficult to assign time limits to any of these divisions since one merges insensibly into another. In discussing fluctuations in abundance of mammals, birds, and other animals in the community under study, reference has been made to certain seasonal changes in numbers. These also constitute parts of seasonal aspects.

The main changes to be noted in the aspect of the forest composing the beech-maple association at North Chagrin are somewhat as follows:

1. *Prevernal aspect.* Although February is usually the coldest month of the year (Fig. 3) and most of its aspects are hibernal, yet in this month mosses and lichens definitely take on new color, and during the latter part of the month, crows and hawks appear. Tufted titmice and cardinals begin to whistle occasional spring-like notes, and the pileated woodpecker becomes noisy. The woods are very wet from melting snow or rains, and standing water in pools is a feature of the aspect.

By the first week in March some of the plants that have carried green leaves over winter, like spring cress and wild blue phlox, or some of the violets, show definite responses in the erection of their stems and leaves, while the green leaves of wintergreen, partridgeberry and trailing arbutus take on new freshness. Although there is much alternation of freezing and thawing during the month the development of herbaceous vegetation is only temporarily checked by low temperatures, and responds rapidly to increasing warmth. Beech nuts and sugar maple seeds sprout in March even though they are bound to be covered with snow or encased in ice before the month is out.

By the latter part of March hepaticas and spring beauties may be found

in bloom—the hepaticas on certain south-facing slopes, and the spring beauties on the less wet places of the higher portions of the area. Certain species of mosses and lichens will be developing their fruiting bodies. *Protococcus* on beech trunks, and the green alga of the temporary pools start new growth. Throughout the month the barred owl has been sitting on her eggs, and both skunk and woodchuck have come out of hibernation. The tracks of raccoons have become common, chipmunks appear in numbers, bird music increases, and woodpeckers indulge in much drumming.

Unless delayed by snow or unduly low temperatures a great change takes place in the aspect of the forest during the latter part of March and the first of April. The higher land begins to green with the developing leaves of yellow adder's tongue, cut-leaved dentaria, and spring cress. Many plants of spring beauty come into bloom but they do not add appreciably to the green of the forest floor as the color of their leaves is more red than green. Many other plants are now recognizable. The spikes of both red and white trillium are emerging, rue anemone is in the "grape" stage, sweet cicely, Canada violet, blue cohosh, early meadow rue, golden seal, wild leek, wild blue phlox, swamp buttercup, and dutchman's breeches may all be recognized by the practiced eye. The heart-shaped cotyledons of seedling jewelweed are thickly scattered in certain locations. Many clumps of hepatica in bloom may be seen in favorable situations. The flower buds of elms and red maples are large and swollen, and gray squirrels begin to cut them down for food. The voice of *Hyla crucifer* is added to the early spring bird music. On the lower levels near the ground are many insects, particularly mosquitoes, small flies, small bees, and larger honey bees. Mourning cloak, question mark, and red admiral butterflies may be seen. The winter bird companies begin to break up.

By the second week in April the greening of the forest floor has progressed considerably. The foliage of spring beauty, spring cress, cut-leaved dentaria, dutchman's breeches, hepatica, and other plants has now definitely occupied the ground. This is the beginning of the "wildflower" display. From April 10 to 15 hepaticas will be at the height of their blooming season, and so quickly does the peak of their blossoming time pass, that one of these days will stand out above others for the abundant display that it offers. Spring beauties will begin to occupy the ground with their pink and white blossoms a few days later. Both these plants close their flower-heads on overcast, rainy, or cloudy days, so that their color pattern on the forest floor may be withdrawn at times. If snow comes, their flowers or leaves will often be seen protruding from the surface of the white blanket. The woods are still wet at this time of year, and standing water continues in the surface pools.

The buds of the forest trees are swelling now and so adding a new note

of color to the upper stories of the woods. Red-berried elder is sprouting vigorously. Fly honeysuckle comes into bloom. The leaves of wild black cherry break from the buds. The round-leaved violet comes into bloom, the flowers appearing before the leaves.

Titmice are constantly calling and woodpeckers drumming. The first of the summer resident birds—the phoebe—may be found about the wet places where insects are on the wing. The temporary pools swarm with minute forms of plant and animal life. As increasingly more sunlight reaches the forest floor through the leafless branches of the trees, differences in humidity as between day and night often become extreme. By the latter part of April yellow adder's tongue reaches a climax of bloom so that certain places are suffused with its yellow color. Red trilliums are now at their best, and some white trilliums are blossoming. Leaves of May apple begin to be noticeable. The breaking of the leaf buds on the trees gives the branches a filmy appearance and the sky begins to be shut out a bit.

The first week in May marks the high tide of the wild-flower display in the beech-maple association. The great white trillium now occupies the center of the stage and many of the less numerous species are in bloom. Spring beauty spreads itself like a pink carpet on the higher lands. The forest floor seems to be fully occupied with herbaceous growth, and sprouting seedlings of beech and sugar maple are recognized by their cotyledons. The buds on the forest trees now begin to break, and on a certain day the air will be filled with the falling bud-scales of beech. When viewed from a distance these opening buds give characteristic color to the forest trees. Brown indicates beech; green, sugar maple; and red, red maple. Both the beech and the sugar maple now come into bloom—the blossoms of the sugar maple imparting to the trees a brilliant yellow-green color in sunlight. Gray squirrels will be noted in the tree tops feeding upon beech blossoms.

This is the time when the summer resident birds appear, and when the woods may be flooded with warblers and other transient species. On the newly developing foliage tiny caterpillars appear, and in the air there is a surge of newly awakened insect life. Permanent resident birds are already nesting.

In the beech-hemlock association the Canada mayflower is the only herbaceous plant that forms a ground cover. Spikes of this plant appear in late April and the flowers begin to open about May 15.

2. *Vernal aspect.* The aspect of the forest is now rapidly changing, due to the unfurling of the leaves on the trees. Those on the lower levels are the first to expand, making a story of green below the tree tops. About the 10th or 11th of May occurs a day when the trees are hazy with the yellow-greens of newly unfolding leaves. During the time of leaf development on the trees the great white trilliums begin to turn pink and then to fade. As

they pass, the floor of the woods again takes on a yellow hue as three species of yellow violets come into their full flowering season. After them comes the time of flowering of wild blue phlox and wild geranium, but these plants are not in sufficient numbers to add much color to the picture. Seedlings of sugar maple and beech now contribute a good deal of green to the floor of the forest as the earlier herbaceous plants disappear. The green of new leaves of hepatica and May apple also add to the green mantle. From now on the flowers of the herbaceous vegetation are of the more inconspicuous types. The elms and the red maples have already shed their seeds.

As the leaves on the larger trees of the forest develop, less and less blue sky can be seen, until there arrives a time in the latter part of May when the fully expanded leaves shut out the sunlight altogether. The woods are now dark, even at mid-day. This is the time when the spring chorus of the chipmunk reaches its crescendo. These animals are very much in evidence as the dense curtain of foliage shuts the arboreal squirrels from view. The poikilotherms—pilot blacksnake, frogs, toads, salamanders, and snails—are now noticeable. The month of May also witnesses the great northward flight of the transient bird group. Warblers will be noted in the woods, and sparrows under the grape tangles and other débris. It is during the first two weeks of May that the summer resident birds are occupying their breeding territories. The woods are vocal now with bird songs. Insects become abundant. The Acadian flycatcher and the wood pewee complete the list of the summer residents. Now comes the great period of nest building and incubation of eggs. The barred owl, nesting earliest of all, has brought off her brood of three young by the last of April, and now they may frequently be located in the twilight as they beg for food. Young hairy woodpeckers become noisy in their nest holes.

May and June are periods of intense activity among the birds of the area and everything seems to be tense with the pressure of the advance of the season. Both permanent and summer resident species, having appropriated their share of the available nesting territory, are absorbed in the task of reproduction and the placing of their young upon a semi-independent footing in the community. Population density of breeding birds and mammals is at its maximum by the middle of June. Territory lines have been strictly drawn until now, but are relaxed as the summer resident birds bring their young off the nests. This change has already taken place in the case of most, if not all, of the permanent residents. Young gray squirrels, red squirrels, and chipmunks are very noticeable. All hibernators are active and migration is at a standstill. Food is abundant, and the amount of insects consumed must be enormous. Predators, with their own young to provide for, are very active. On days when the humidity is high, frogs, salamanders, snails, and slugs may be found. But this climax of activity quickly passes.

Mortality of young is high, and the moving of the summer bird population
out of the area begins quickly.

3. *Aestival aspect.* By the 20th of June a change in activities is notice-
able, particularly as regards the bird population, as the summer residents
begin to move. Of these the redstart is the most hurried in its departure,
young and old quitting the area by the end of June, after a stay of but a
little over 60 days. A few redstarts will be seen later but these are prob-
ably transients or delayed nesters. The oven-birds follow closely upon
the heels of the redstarts. The first week in July sees them practically gone.
By the end of July the red-eyed vireo and the wood thrush have moved out.
Certain pairs of birds, unsuccessful in the first attempt to raise a family,
persist through three, or even more trials, thus prolonging the stay of a
small portion of their group through July, or even longer. But by August
most of the summer residents have gone.

By mid-June many bird songs are shortened or greatly modified, and
many species have become quite silent. This is often a period of dry weather.
The pools dry up, the withered plants of May apple and cut-leaved dentaria
lie yellow and prostrate upon the ground, the green carpet of May is re-
placed by one of rich brown as the dead leaves of last autumn are exposed
except where seedling beeches and maples have taken their stand. What
vegetation of herbaceous character remains begins to look tattered and shop-
worn. Forest fruits are developing and squirrels are already cutting down
the unripe beech nuts, hickory nuts, and acrons. Tupelo is shedding
some scarlet leaves. The round-leaved green orchid and the nodding pogonia
belong to the aestival aspect of the forest as they come into bloom at this
time. Purple martins and chimney swifts, hunting above the forest roof,
now testify to the fact that insects are flying overhead in the sunshine. Tufted
titmice may be observed shepherding their families noisily about. A cardinal's
tail feather on the ground suggests that this is the period of moulting and
aestivation, and shortly chipmunks disappear into their underground quar-
ters. Temperatures are high, the cicadas are noisy, "punkies" *(Culicoides)*
become very annoying to humans.

4. *Serotinal aspect.* From mid-August to late September the forest
seems silent and deserted. Nesting territories are now disregarded and
there is apparent a tendency for birds to travel together in groups. Wander-
ing families of nuthatches, titmice, and chickadees are encountered. If there
are moist places in the woods the woodcock is liable to be found here. Nests
of the paper wasp have now assumed large proportions. As the fruits of
tupelo, hemlock, cucumber, and the oaks develop they are prematurely gath-
ered by blue jays, gray squirrels, red squirrels, and chipmunks. Not only
is there an immense amount of fruiting and seeding of forest trees, but also
of herbaceous plants. Mushrooms become a feature of the aspect, often in

brilliant colors, and miniature forests of beech drops occupy large spaces
about the bases of the beeches. Again the chipmunks, now emerging from
their period of aestivation, yield to the ecstasy of the spring chorus. The
first migrant birds of autumn—certain warblers, and later, the brown
creeper and the golden-crowned kinglet—appear. Black-throated green war-
blers become briefly abundant beyond the numbers of the summer resi-
dents as the southward movement of the species as a whole begins. An in-
spection of Figure 16 will show that this is a period of low bird population
numbers with the flow of bird life constricted into a narrow channel. But
in September the stream widens and a period of great unrest is ushered in.

5. *Autumnal aspect.* In late September there are chilly days, and the first
of the winter visitors among the birds appear. By the first week in October
the few lingering hooded warblers and scarlet tanagers have gone, and other
summer resident species are probably represented by late migrating in-
dividuals only. The first robins and thrushes are noted in the woods—the
prophecy of many more to come. October sees great flocks of them—robins
in two great waves, the flocks numbering hundreds—and thrushes—her-
mits first, then olive-backs, veerys, and gray cheeks. They feast upon the
wild grapes, the fruits of tupelo, sassafras, pokeweed, and flowering
dogwood. They also give the floor of the forest a thorough looking over
for beetles, grubs and other insects, as they turn over the dead leaves and
dig into the rich humus. Their stay lasts into November, covering the
period of the great fall of leaves from the deciduous trees. Meanwhile the
winter visitors are increasing in number, and if the red-breasted nuthatch
is present, these numbers may reach considerable proportions. The char-
acteristic winter bird companies are now formed and will keep together
throughout the winter.

Color in the forest in autumn develops later than it does along the road-
sides, and many trees retain their leaves long after the roadside trees are
bare. Elm, tulip, and spicebush begin the process by yellowing early.
October 10th sees the first splashes of real color inside the forest, though it
will be ten days at least before the woods are all red and gold. Robins are
noisy, sounding alarms, calling, and occasionally carolling a bit. Chip-
munks add to the racket, chippering and clucking everywhere, and are very
active about the grape vines. Both red and gray squirrels are vocal. Blue
jays are calling, white-throated sparrows singing in the grape tangles,
nuthatches signaling from nearby trees. The green leaves of wild ginger
are still bright in places where this plant occupies the ground.

By mid-October, though the interior of the forest is still predominantly
green, the tops of the trees show yellow, bronze, and red. The tupelos
are quite red. By October 27th the leaves are about half off the trees, and
now rains and high winds will begin stripping off all those that have loosened

their grip upon the twigs. In the absence of wind the leaves will fall lazily by ones and twos. Sugar maples and beeches are the last to surrender their leaves to the winds and often small beeches will retain their leaves, dead and brown, throughout the winter. These newly fallen leaves make a transitory carpet of red, yellow, and brown on the forest floor. With the falling of the leaves of the primary dominants beech nuts and maple seeds also are shed in large quantities, and storage activities on the part of chipmunks, red squirrels, and gray squirrels becomes a major activity. Numbers of gray squirrels may increase as individuals from outside the area come in attracted by the abundance of food. There is liable to be a full chorus of chipmunk clucking which may be taken up and carried throughout the entire range of woodland as far as the ear can discern it.

The first week in November sees the forest floor first yellow, then changing through bronze to brown. There are large open spaces in the forest roof, and the dark green of hemlocks begins to show in the background as one faces the areas where the beech-hemlock association has its stand. Voices of towhee, nuthatch and junco are characteristic of this period, and bob-whites may come into the deep woods attracted by the beech nut supply. The trees will be bare by the third week in November. This is still a period of great activity among birds and mammals, and there are days when they are very vocal, and when *Hyla crucifer* adds his voice to the chorus.

6. *Hibernal aspect*. There is no sharp demarcation between autumnal and hibernal aspects. Indian summer days may be extended through November, though snow usually comes before the month is well advanced. Tree trunks are now a feature of the aspect, the light gray of beech and the dark brown of sugar maple making a fine contrast. With the coming of the first real snow-blanket the woods present a record of moving animal life written upon its white surface. This is one of the characteristic aspects of winter. At times the tracks of gray squirrels will cover every part of the area. These animals, with red squirrels and chipmunks, will be noted abroad throughout the winter, and will write most of the story on the snow. Tracks of cottontail rabbit, red fox, white-footed mouse, and short-tailed shrew will be commonly seen. This is the time of hibernation for invertebrates and some vertebrates as well. In December, January, and February the species list of birds is restricted to the permanent resident and winter visitor groups, with a massing of numbers in December and a low point in late January.

A feature of the hibernal aspect is made up of the green leaves which a number of plants carry over winter. Prominent among these is the hepatica. Others are foam flower, bishop's cap, wild blue phlox, spring cress, and some violets, together with christmas fern, spinulose wood fern, marginal shield fern, and shining club moss. The sedge *Carex* shows green clumps

throughout the winter along the edges of the ravines. As the winter progresses the débris of stored foods appears where it is dug up and consumed by the squirrels, and one can form a fairly good opinion as to just what foods are mostly depended upon for winter needs.

Winter in the area under study is a period of high humidity, due to the fact that snow does not usually stay upon the ground for any great length of time, and temperatures are frequently above the freezing point. This means much melting of ice and snow and much standing water in pools. The atmosphere is often filled with mist and the snow saturated with water.

PLANTS AND ANIMALS

The fundamental difference between plants and animals is, of course, that plants manufacture their own foods out of elemental substances, while animals do not, but must in the last analysis depend upon the products of plants for their supplies of food. Seasonal behavior on the part of the animal population of a biotic community is thus closely correlated with seasonal changes in plant activities. Aspection, from the standpoint of the animal population is but a shifting of food supplies—a sort of clearing and resetting of the table. On the other hand, in their search for and gathering of food, and through other activities, animals in turn affect plants in various ways.

Seasonal responses of animals to the activities of plants are well illustrated in the present study. Such responses may be direct, as when the animal is directly dependent upon plant materials for food, or indirect, as when the animal is dependent upon other animals for its food. The following sequence of observed events in the area under study is illustrative of such relationships.

With the blossoming of the early wildflowers in April winged insects appear. These are attracted to the pollen and nectar offered by the flowers, and their activities assist in the cross-pollination of the plants. The phoebe (a flycatcher) now comes into the woods, feeding upon the flying insects as an acceptable food supply.

With the swelling of the buds on the forest trees in spring, gray squirrels climb aloft to sample this new offering of food, and such birds as the purple finch and the rose-breasted grosbeak make their appearance as consumers of this plant product.

With the expansion of the leaves on the trees, hatching insect eggs produce a multitude of caterpillers as consumers of new foliage. With the appearance of this new food supply for birds, come hosts of migrating warblers whose arrival is neatly timed to coincide with the opportunity to glean many of these minute larvae from the developing foliage. The summer resident birds, all highly insectivorous, now arrive from their southern winter-

ing quarters and replace the early transients as consumers of enormous numbers of insects.

With the storage of carbohydrates in roots, tubers, and other underground structures of herbaceous plants, chipmunks begin to nose the ground and to plow up many of these crisp foods. They also feed upon blossoms and developing seeds.

With the ripening of forest fruits, birds and rodents become very active about the bearing trees and vines and lesser growth as they feast upon these newly offered foods.

With the development of the great forest crop of gilled mushrooms, a new assembly of insects becomes active as a consumer of this plant product, and many rodents also seek it out as a new food.

With the falling of nuts and seeds from the trees, activity on the part of mice and squirrels becomes strenuous as they gather these staple foods for storage against future needs.

With the arrival of winter inactivity in the plant world the animal population exhibits a number of differing responses to this radical change in conditions. Some species migrate to other places, some go into hibernation, some live upon the stored food which they have gathered and laid away, some increase their resistance to lowered temperatures and go on hunting as before.

Basically the forest dominants must be considered as the determiners of the whole complex of life within the range of their influence. They, of course, depend upon soil and climate for their existence where they are, but being there, they not only *limit* and *circumscribe* the life activities of other organisms associated with them, but *vitalize* them as well. The limiting influence of the forest on other organisms is expressed through such things as occupation of the ground, cutting down of light, increasing relative humidity, reducing rate of evaporation, modifying temperature—matters which in the present study have been considered under the head of climate. Species which are not equipped to live in such an environment are excluded. The vitalizing influence of the forest is expressed through the production of stored energy of such quality and quantity, and in such form, as to be readily available to the animal population as food.

The beech-maple forest thus limits and supports an enormous insect population which not only consumes vast amounts of plant material, but which also has many complex interrelations within its own group and with other animals; a rodent population adapted to the use of beech nuts and sugar maple seeds; a shrew population that spreads its network of tunnels beneath the humus for the capture of insects and other prey; a woodpecker-nuthatch-flycatcher-thrush population adapted to the capture of insects in many different situations above ground; and a relatively small carnivore

group which subsists upon the smaller vertebrates. The mammals are predominantly seed and insect eaters, the birds predominantly insectivorous. Chains of animals are thus linked together by food, and all dependent in the long run on plants. Thus we have the concept of the food chain and the food cycle (Elton 1927).

In addition to an adequate food supply, the numbers of animals to be found within a forest community are greatly influenced by the facilities offered for successful reproduction and for protection from enemies. From the standpoint of birds and mammals this means cover, nesting sites, nesting materials, and satisfactory adjustment to the environment during the breeding season. It is because the forest under study is rich in these respects that such a large animal population as has been noted at times is possible.

From the standpoint of the effects of animal activities upon plant life the fact of outstanding significance is the very large consumption of plant materials by insects. Not only is the steady consumption of foliage by the larvae of many species involved, but no part of the plant structure is immune from attack. Buds, leaves, blossoms, bark, sapwood, heartwood, twigs, leaf petioles, root structures, seeds, juices—all have their specialized groups of insects adapted to feed upon them, or to utilize some of them for purposes of pupation or hibernation. The effects of such activities on plants are essentially destructive.

Over against this potentially grave destructive force, and mitigating its effects in large degree, is the ever-present fact that insects are hunted and consumed as food by practically the entire bird and mammal population, the entire spider population, and a considerable group within their own ranks. It is to this insect-consuming group of animals that the forest owes its continued existence, for it seems a fair assumption that if the activities of the birds and mammals and predaceous insects of the forest community were withdrawn or nullified in some way, the forest would soon be destroyed by the unchecked ravages of phytophagous insects.

It is true that many birds and mammals are also consumers of buds, leaves, shoots, bark, and roots of plants. While all of this has its limiting effect on plant life, it is inconsequential as compared with the effects of insect consumption of plants or of competition among plants themselves. The large consumption of seeds by birds and mammals is also inconsequential, except possibly in years of low seed production, as seeds are produced normally in enormous quantities and there is a very large surplus over and above the needs for reproduction. In fact, with the ever-present threat of serious injury to the forest dominants through the destructive activities of insects, the conversion of the surplus seed supply directly or indirectly into insect-consuming animals appears as a necessary protective

measure and a part of the mechanism whereby equilibrium in the community is maintained.

The animal population of the forest may thus be considered in relation to its effect upon plant life from two points of view—primarily as a severely limiting or potentially destructive force, as represented by the phytophagous insects, and secondarily as a protective and conserving force, as represented by the predaceous insects, spiders, birds, and mammals. In this connection it is interesting to consider how largely insects enter into the regular diet of animals usually classified as more or less strictly herbivorous or carnivorous.

The storage of nuts underground by squirrels has often been referred to as a kind of "planting" of seeds, beneficial to the forest, when such seeds are not later dug up and eaten but are left to sprout. This may be the case in areas where reforestation is in progress, but in the already established forest it is negligible as compared to the natural and normal seeding of the forest trees which is usually far in excess of the need.

An important contribution made by animals to the well-being of the plant community which should not be overlooked lies in the vast amount of stirring up of the soil that they accomplish. Shrews, mice, moles, and chipmunks are great tunnelers in soil and humus and dead wood. Many invertebrates, like the ants that work in dead wood, the insects that live under dead bark, earthworms, and many animals of minute size that are active in the humus (Jacot 1935), all contribute to this result. The plowing of the ground by red squirrels and gray squirrels as they prosecute their search for buried food is somewhat in the nature of continuous cultivation, and there is constantly added from their droppings, and from those of countless other animals, an enrichment of the soil that in the aggregate must bulk very large. Some of this stirring up of the soil is of benefit to the more deeply rooted plants in freeing them from competition with more insecurely rooted neighbors. Thus the chipmunk, nosing out the tubers of spring beauty or dwarf ginseng, makes better the conditions for growth for the seedling beech crowded in among the vigorous herbs.

Because of such interrelations plants and animals form a sociological unit, the biotic community, making a consideration of either without the other incomplete.

SUMMARY AND CONCLUSIONS

The subject of the study herein presented is a 65 acre tract of beech-maple-hemlock forest in the Cleveland, Ohio, Metropolitan Park System. Systematized work was carried on through regular weekly visits covering a period of four years. Records of temperature, precipitation, relative humidity, wind velocity, and evaporation rate were obtained.

2. Considering the vegetation of the area as a whole, it is evident that there exist here two rather distinct forest communities; a beech-maple association and a beech-hemlock-oak-chestnut mictium.

3. The beech-maple association represents the climatic climax of the region. It is mature, vigorous, stable, well established, and occupies 89 per cent of the area. It is characterized principally by the beech and the sugar maple as primary dominants, with red maple, tulip, white ash, and northern fox grape as secondary dominants. Shagbark hickory, cucumber, red oak, and white oak are listed as incidental dominants, and hop hornbeam and American hornbeam as subdominants. Other subdominant species include 12 of shrubs, 69 of herbaceous plants, 14 of ferns, 7 of climbing, twining, or trailing plants, 10 of mosses, and 6 classified as miscellaneous. Of saprophytic and parasitic plants 247 are listed. Seasonal aspects, including the responses of both plants and animals to seasonal changes, are described.

4. The beech-hemlock-oak-chestnut mictium represents a remnant of former forest communities now giving place to beech-maple. It is unstable, lacks vigor, is not well established, occupies 11 per cent of the area. It is characterized principally by the beech, the hemlock, and formerly the chestnut, as primary dominants, with red maple and red oak as secondary dominants. Shagbark hickory, cucumber, tupelo, sassafras, white oak, wild black cherry, pignut, black birch, and scarlet oak are listed as incidental dominants, and hop hornbeam and American hornbeam as subdominants. Other subdominant species include 7 of shrubs, 1 of climbing plants, 6 of herbs, and 5 of ferns.

5. One of the primary dominants of the mictium, the beech, represents the entering wedge of the climatic climax. Another, the hemlock, represents a more northern forest community left in its present position apparently as a remnant of the forest which followed the glacial ice in its northward retreat. In this community the presence of certain subdominants usually associated with hemlock is noted. The oak-chestnut remnants on the other hand represent a prominent forest community now to be found in the southern Appalachians.

6. As compared with the plants of the area the animal content presents a constant fluctuation in numbers, species, and activities. A study of the vertebrates and some invertebrates discloses the presence of 27 species of mammals, 83 of birds, 8 of reptiles, 11 of amphibians, and 20 of molluscs.

7. A study of the numbers and distribution of these animals indicates that all habitats and ecological niches in the area are well occupied when the population is at its peak, but that great changes in numbers occur both seasonally and annually. The most abundant mammals were found to be the short-tailed shrew and the white-footed mouse. Of birds 11 species were

classed as permanent residents, 8 as autumn and winter visitors, 16 as summer residents, 23 as transients, and 25 as occasional visitors. The number of nesting pairs per acre was found to average 2.3 (5.7 per hectare). Of the reptiles only one, the pilot blacksnake, was found to have important ecological relations.

8. The constituent animal species, exclusive of invertebrates, classified on the basis of abundance, activities, and influence in the community were assigned the following positions: permanent predominants 7, fluctuating predominants 3, seasonal predominants 15, permanent members 11, fluctuating members 2, seasonal members 47, incidental members 37.

9. The interrelations between plants and animals are considered, and the conclusion is reached that a consideration of either without the other is incomplete.

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MOISTURE RELATIONS IN THE CHAPARRAL OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

By

HARRY L. BAUER
Santa Monica, California

CONTENTS

MOISTURE RELATIONS IN THE CHAPARRAL OF THE SANTA MONICA MOUNTAINS, CALIFORNIA

INTRODUCTION

Chaparral is found extensively in California, especially in the foot-hills and mountain ranges of lower altitudes in the coastal portions of the central and southern parts of the state where it is a climatic climax type of vegetation. The most conspicuous characteristic of this community is the mass dominance of broad-sclerophyll shrubs.

As the chief vegetative cover of the watersheds of southern California, chaparral is of great economic importance in that it lowers the loss of water through surface run-off, increases the flow of clear water in streams, and decreases the probability of serious floods and erosion.

The investigation herein reported is concerned primarily with the mois-ture relations in a representative area of Californian coastal chaparral. In the first part of the paper there is a somewhat detailed account of the structure and other ecological features of this community. Following this, the environmental complex of the association is analyzed with particular reference to soil moisture and the evaporating power of the air as they are related to growth and other features of the vegetation. Consideration is also given to precipitation, atmospheric moisture, and temperature, espe-cially soil temperature. An attempt is made to evaluate the several factors and to correlate them with the activities of the vegetation.

Instrumental work was begun with the week ending September 5, 1931. In all, fifteen research stations were utilized. These stations were visited and data collected weekly for an unbroken period of fixty-six consecutive weeks. After this four stations were selected for further observation. At these stations measurements were made at four-week intervals throughout the second year, terminating on August 28, 1933.

REVIEW OF THE LITERATURE

The first studies of chaparral were made from the standpoint of geog-raphy, taxonomy, and forestry. With few exceptions, noteworthy ecological investigations have been made only within the last decade. Of the accounts of the early European botanists who described the vegetation of western North America, that of Schimper (1903) was the first to be at all satis-factory. McKenney (1901) described in detail the several chaparral "for-mations" in the Santa Ana Mountains, California.

Leiberg (1899, 1900) described the chaparral of certain forest reserves. A number of minor articles by foresters and taxonomists appeared previous to 1920.

The first papers by Californian botanists were of a phytogeographical nature. Hall (1902) studied the chaparral zones of Mt. San Jacinto, and Parish (1903) and Abrams (1910) published descriptions of the scrub communities of the entire southern portion of California. Clements (1920) also described the communities of this area.

The first monographic ecological study was by Cooper (1922). In this, the Californian chaparral is considered from a number of different angles and there is included an account of intensive instrumental work on a representative area near Palo Alto. Shreve (1927) published the results of some instrumentation in the vegetation, chiefly chaparral, of the Santa Lucia Mountains, and Howell (1929) described the chaparral of Santa Ana Canyon. Papers by Whitfield (1932) were on transpiration and osmotic pressure in the chaparral near Santa Barbara, California, and one by Copeland (1932) was on transpiration and temperature in the chaparral of the northern Sierra Nevada. Shapiro and de Forest (1932) reported the results of transpiration studies in the chaparral of the eastern Santa Monica Mountains.

THE AREA

LOCATION AND TOPOGRAPHY

The Santa Monica Mountains, one of the outer coastal ranges in southern California, extend westward of the city of Los Angeles for about fifty miles. The main axis of the range is located at approximately 34° 5′ north latitude and its center is near 118° 40′ west longitude. The map (Fig. 1) shows the location and the relation of these mountains to some of the geographical and topographical features of this section of the state. It may be noticed that, unlike most Californian ranges, this one trends in an almost straight east-west direction. The Pacific Ocean lies along a considerable portion of the southerly base of the range and the San Fernando Valley along the northerly.

The topography of the area is rough. The highest peaks, which reach an altitude of about 3,000 feet, are located within three or four miles of the ocean. After the storms of the rainy season, the streams carry a large amount of water, but for the greater part of the year most of them are dry and the others carry such a small amount of water that those on the seaward side cannot keep their channels through the beach sand clear as far as the ocean, consequently forming lagoons bordered with a rank growth of vegetation that is in striking contrast to the chaparral on the nearby dry slopes.

The chief geological formations, the Topanga and Modello, are of the middle and upper Miocene origin respectively (Hoots, 1930, p. 88). The last anticlinal uparching of these mountains occurred in the late Pleistocene.
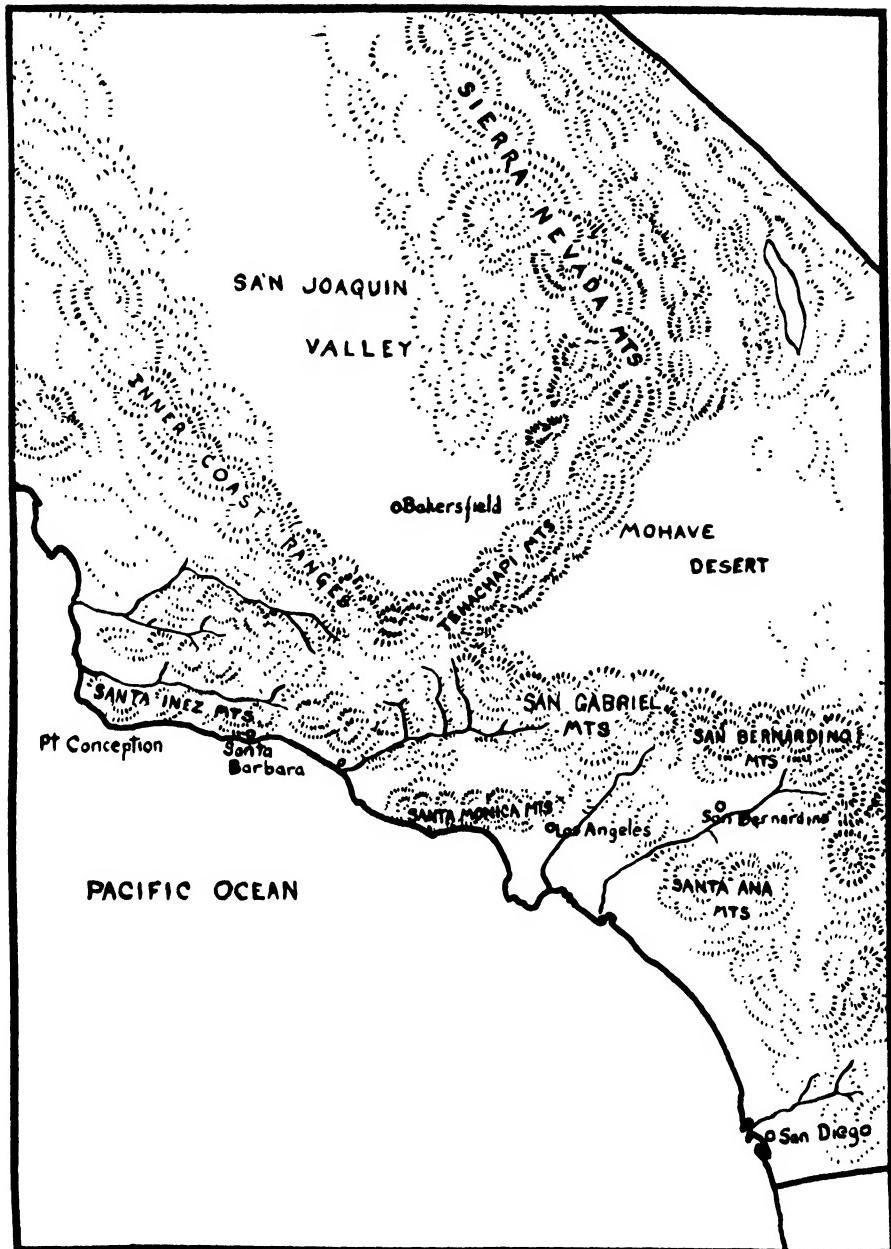
FIG. 1. Southern California showing the location of the Santa Monica Mountains, and their relation to other features.

The soils of most of the area are classified (Nelson, 1920) as "rough, broken, and stony land"; outcrops of rock are common. The layer of fine soil that has accumulated at some places within the mountain complex is

seldom more than a few feet in thickness. The alluvium at the bases of the mountains is much thicker but has no direct bearing on the chaparral of this study. Since the slopes are steep and the drainage generally good, accumulations of alkali do not occur in the soils of the area.

THE CLIMATE

The climate of the Santa Monica Mountains and of southern California in general is one of mild wet winters and hot dry summers, frequently designated as "Mediterranean climate." This climate, as it is found in California, has been carefully described by Russell (1926). The climatological records of the Los Angeles station of the United States Weather Bureau, which cover over half a century, are fairly applicable to the Santa Monica Mountains as to principal variations, although not necessarily as to exact amounts or intensities. These records show January to be the coldest month, having an average mean temperature of 55.1° F. August is the warmest month, having an average of 71.3° F.

The average annual precipitation at Los Angeles is about 15 inches per year, but in the nearby mountainous areas it is considerably greater, ranging up to 30 inches per year. More than 90 per cent of it comes during the six months, November to April. The average summer is practically rainless, having less than 2 per cent of the annual precipitation in the four months, June to September. Schimper (1903, pp. 465-469) has shown that each of the five widely separated chaparral areas of the world is correlated with a climate similar to that of the area here considered.

SITES FOR INSTRUMENTATION

The instrumental area was near the geographical center of the Santa Monica Mountains and is believed to represent well the chaparral of the entire range and also to be fairly characteristic of the coastal chaparral in general. According to Cooper's map of species density (1922, plate 1) this area lies just outside the region of greatest density, a region in which the vegetation is characterized by having from 21 to 25 chaparral species. The particular section chosen for instrumental work lies mainly along the ridges that lead toward Saddle Peak, and partly within Topanga Canyon.

The central part of the Santa Monica Mountains is traversed by a number of roads and a more or less elaborate network of firebreaks and trails constructed chiefly as a means of fire protection. The area is thinly populated, places of habitation being confined to a few summer resort subdivisions in the deeper canyons and a few widely scattered ranches. It is believed that the vegetation here has been very little disturbed by human activity.

The stations were established so as to represent varying conditions of vegetation, elevation, slope exposure, proximity to the ocean, and other

features.   Stations 1 and 14 were near the ocean beach and not far above sea-level.   Station 2 was about two miles inland and near the bottom of Topanga Canyon.   Station 15 was near the base of the inland slope of the mountains and quite removed from the direct influence of the ocean.   The remaining eleven stations were all located along a ridge of about 2,000 feet elevation and about three miles from the ocean.   Of these, numbers 3 and 9 were near each other and on an area where the above-ground parts of the plants had been completely destroyed by fire one year previous to the beginning of the investigation.   Station 4 was only about 50 feet from Station 3 but was located in characteristic chaparral that had not been burned in recent years.   Stations 6 and 7 were established as characteristic easterly and westerly exposures, respectively, but were abandoned after four months because they were too greatly influenced by the conditions of the nearby general northerly exposure on which Station 5 was located.   Stations 7, 11, 12, and 13 were all very similar except as to the direction in which the slopes faced, the four stations representing the four cardinal exposures.   A summary of information on the stations is furnished in Table 1.

THE VEGETATION

COMMUNITIES ASSOCIATED WITH CHAPARRAL

The term chaparral has been used in a number of different ways.   Some writers have applied it to any type of shrubby vegetation, even the desert scrub of the arid southwest.   Clements (1920) uses the term in a broad sense and divides the community into two associations, (1) Petran chaparral, deciduous thickets found extensively in the Rocky Mountains, and (2) Coastal chaparral, the broad-sclerophyll vegetation of southern California. Jepson (1925) describes two types of chaparral in California, namely (1) soft chaparral, composed chiefly of deciduous species in the northern part of the state, and (2) hard chaparral, the same as the "coastal chaparral" of Clements.   Cooper (1922) would restrict the use of the word to com munities dominated by broad-sclerophyll shrubs, and recognizes two such associations in California, namely (1) climax chaparral, found especially in the southern part of the state, and (2) conifer forest chaparral, a successional form found associated with conifer forests in the northern part of the state.   When the term chaparral is used alone in this paper, it refers to the coastal chaparral of Clements, the hard chaparral of Jepson, and the climax chaparral of Cooper, this being the ubiquitous plant community in the area considered.

In addition to the widespread chaparral, a few minor communities are present in restricted extent, namely (1) broad-sclerophyll woodland dominated by *Quercus agrifolia*,[1] (2) coastal sagebrush composed chiefly of

[1] All plant names are according to Jepson (1925).

Table 1. Summary of station data.

Station	Eleva-tion ft.	Slope		Vegetation	Comments
		Degrees	Exposure		
1...	85	35	S	Coastal sagebrush.	"Sea-level" station. Near beach. Unprotected from ocean.
2...	400	35	S 5°E	Ceanothus type chaparral.	"Canyon" station. Topographic-ally protected on three sides.
3...	2150	10	S 25°E	Recovering from recent burning.	"Burned chaparral" station. Plants sprouting from roots. Much bare ground.
4...	2150	10	S 35°E	Adenostoma type chaparral.	Characteristic unburned chapar-ral.
5...	2200	20	N	Quercus-Adenostoma type chaparral	Representative northerly slope.
6...	2200	23	N 70°E	Adenostoma type chaparral.	Similar to 5; better protected.
7...	2200	22	N 70°W	Mixed chaparral species	Similar to 5; nearer ravine.
8...	2350	21	N 15°E	Quercus-Ceanothus type chaparral.	Tall chaparral of northerly slope.
9...	2100	17	N 35°E	Same as 3.	Same as 3.
10...	2200	10	N 90°W	Adenostoma type chaparral.	Representative westerly slope.
11...	2300	17	N 90°E	Adenostoma-Cean-othus chaparral.	Representative easterly slope.
12...	2375	25	N 90°W	Adenostoma type chaparral.	Representative westerly slope.
13...	2350	26	S	Adenostoma type chaparral.	Representative southerly slope.
14...	160	23	S	Ceanothus type chaparral.	Near 1 and a check upon it. Slightly better protected.
15...	1060	12	N 35°E	Mixed chaparral species.	At edge of San Fernando Valley. No direct ocean influence.

Salvia mellifera, Eriogonum fasciculatum, and *Artemisia californica,* (3) riparian or streamside association in which *Alnus rhombifolia* and *Platanus racemosa* are the most important species, and (4) a few small islands of grassland, doubtless the result of fire or other disturbances.

The ecotone between chaparral and the broad-sclerophyll woodland is not wide, the characteristic species mingling to only a very slight extent. However, between the chaparral and the coastal sagebrush, which usually occurs as a narrow zone at the lower edge of the chaparral where conditions are slightly more xeric, the boundary is very poorly marked, the chaparral appearing to be invading the sagebrush. This mingling is doubtless evidence of seral relation between the two communities.

Ecological Structure of Chaparral

The most conspicuous feature of chaparral is the abundance of shrubs with broad evergreen leaves. In this growth trees are almost excluded and herbaceous plants are not abundant except along roads or other places where disturbances have occurred.

Under ordinary conditions the shrubs in this chaparral attain a height of about 2 m. Where exposed to the direct ocean winds they may be less than 1 m. and on the more favored northerly slopes they may be over 4 m. in height. Nevertheless the general appearance and uniformity of the chaparral mantle changes but little from canyon slope to hilltop. Something of the appearance of chaparral is shown in the photographs (Figs. 2 and 3).

Extensive studies of successions in chaparral have not been made. Some botanists question the climax character of the association, believing that, if it were not for the constantly recurring fires, the chaparral would eventually be replaced by a tree community. Cooper (1922, p. 82) is convinced that chaparral is a true climatic climax. His conclusion is based on the widespread dominance of this community, its evident stability, the fact that it occurs on sites of diverse soil and topography, and the obvious adjustment of broad-sclerophyll vegetation to climate. No areas can be found where chaparral similar to that of the Santa Monica Mountains is actually being replaced by other communities.

Secondary successions are frequently instituted by fires which denude the ground of vegetation, leaving no evidence of life above the surface (Fig. 9). During the first season after the fire, there usually appears a rank growth of herbs and also rapidly growing sprouts from the root crowns of the burned chaparral plants. The shrubs on the burned area investigated appeared to be about half regrown by the end of the third season after the fire. In a number of other places chaparral that had been burned about ten years previously was found to have resumed a normal appearance.

Transect studies showed that *Ceanothus macrocarpus* and *Salvia mellifera* were more abundant in young than in old chaparral, thus indicating that these species are more important in seral stages than in the climax. This probability is also indicated by the presence of numerous dead specimens in the older, but not younger, areas of chaparral. Shreve (1927, p. 38) notes that stands of certain species of *Ceanothus* serve as a nursery for seedlings of other species, and Cooper (1922, p. 87) states that chaparral with a large proportion of *Ceanothus* is likely to be a stage in secondary succession.

A successional stage five years after the chaparral was cut in the process of road construction is shown in the photograph (Fig. 5). The lighter colored vegetation next to the road is an almost pure stand of *Salvia mellifera*. In the adjacent uncut chaparral, this species did not appear except as small weak specimens. From this it appears that the black sage requires much light and cannot thrive after the chaparral shrubs exceed it in height. Its presence in marked quantity in the chaparral probably indicates fire or other disturbance not many years previously.

FIG. 2. Characteristic chaparral along the road leading to Saddle Peak. Elevation about 2,000 feet. Four stations, one on each cardinal exposure, were located near the top of the hill.

FIG. 3. Chaparral covered slopes of Topanga Canyon. Elevation about 400 feet. The mantle of vegetation has the same uniform appearance generally throughout the range.

FIG. 4. *Ceanothus spinosus* (mountain lilac) in full bloom in March. This shows something of the aspect of chaparral in late winter and early spring.

FIG. 5. Secondary succession after cutting vegetation in clearing road right-of-way. An almost pure stand of *Salvia mellifera* has grown up; climax chaparral above this.

SEASONAL ASPECTS

For a large part of the year chaparral shows little or no change in its appearance. After growth conditions become favorable in the early spring, however, there is a comparatively short period during which stems elongate, new leaves appear, and flowers and fruits are produced.

During the seasons considered in this investigation the flowering period of most species lasted for only a few weeks, but this period was not the same for all species. The result was that flowers were in evidence from January to July. The rather steady succession of flowers on chaparral species is shown in Figure 8. Blossoms appeared on the manzanitas in January before new leaves were produced. The time of greatest flowering activity, as judged by the number of species in bloom, was March and April. By far the most impressive display, however, occurred in February and March when the showy flower clusters on the widely distributed *Ceanothus macrocarpus* and *C. spinosus* seemed to transform the chaparral into a great garden (Fig. 4). Most of the broad-sclerophyll species characteristic of the climax chaparral were found to be in anthesis earlier, and to have shorter flowering periods than the suffrutescent and less sclerophyllous plants associated with the related communities.

FIRES

Fires have always been of frequent occurrence in chaparral. It is known that the aborigines, long before the time of white settlement, often fired the brush (Jepson, 1910, p. 11). Early settlers burned it periodically in the belief that it would improve grazing. In spite of elaborate present-day precautions to prevent them, the number of fires occurring annually in chaparral is surprisingly large. Records from the Los Angeles County Forestry Department show that for the period 1926 to 1934 an average of about 35 fires per year occurred in the Malibu Division of the Santa Monica Mountains, an area of about 200 square miles. Most of these were of insignificant size but one or two per year exceeded an area of one hundred acres.

As a means of determining the age of chaparral, or at least the time elapsed since the last fire, a large number of stems were cut and the annual rings counted. In much of the chaparral of the Santa Monica Mountains, no specimens over 12 years of age could be found. The oldest occurred in the vicinity of Station 8, where it was 26 years old. It is probable that no large percentage of chaparral is older. Lowdermilk (1933), in commenting on an area of chaparral on the east fork of San Dimas Canyon in the San Gabriel Mountains, states that it had not been burned for 50 years and that it had probably escaped fire as long as any chaparral in California.

FIG. 6. Specimen of *Photinia arbutifolia*. During the winter of 1931-32 many plants were undermined by heavy rains and fell into the roads, exposing much of their root systems.

FIG. 7. Station 8; north slope. Elevation 2,350 feet. The ground surface is covered with a comparatively heavy layer of litter and humus. Note the peculiar pitted appearance of the Ceanothus stems.

JAN   FEB   MAR   APR   MAY   JUN   JUL   AUG   SEP

Arctostaphylos glandulosa

Ceanothus macrocarpus   BROAD-SCLEROPHYLL SPECIES

Dendromecon rigida

Ceanothus spinosus

Rhamnus crocea

Cercocarpus betuloides

Rhus ovata

Quercus dumosa

Prunus ilicifolia

Adenostoma fasciculatum

Photinia arbutifolia

Rhus laurina

NON-SCLEROPHYLL SPECIES

Encelia californica

Eriogonum fasciculatum

Salvia mellifera

Pentstemon spectabilis

Eriophyllum confertiflorum

FIG. 8. Flowering periods of characteristic chaparral species in 1932.

All investigators agree that fire has contributed much to the present appearance of chaparral. It is believed to have affected the stature, form, and xeric characteristics of the p'ants. A number of species respond to repeated fires by developing, just below the surface of the ground, large, tuberous platforms, or irregularly shaped masses of woody tissue from which numerous stems may arise. Fires explain the evident lack of uniformity in the composition of chaparral. Two or more contiguous quadrats may show a strikingly different floristic make-up. A fire often does not sweep the area clean, but burns irregularly, leaving islands in the midst of the burned area, as shown in the photograph (Fig. 9). The new growth may be somewhat different from that of the unburned island and, thus, make for a lack of uniformity in the vegetation after recovery from the fire is complete.

TRANSECTS

As a means of getting accurate data on the structure of the vegetation, the line transect was found much more suitable than the chart quadrat. This was because of the great difficulty of plotting accurately the plants in a dense thicket. In running the transects a steel tape was used and a transect unit of 15 m. selected. Only the woody plants were considered. The actual distance that each plant spread over the line was recorded, thus giving a better basis for ascertaining the relative abundance of species

FIG. 9.   Burned area near the site of Stations 3 and 9.   Note the islands of unburned vegetation.   Photographed a few weeks after the fire of August, 1930.

FIG. 10.   Station 8; southerly exposure.   Elevation 2,350 feet.   Note the wooden standard used to support atmometers at different levels.   Plants were held back when the picture was taken.

than would be the case if the plants were only counted and their size disregarded.

A tabulation of the results of 1,065 m. of line transects is furnished in Table 2. This includes various elevations, exposures, and localities but excludes measurements made on recently burned areas or other areas that for some reason were not representative of the true coastal type of chaparral.

TABLE 2. Summary of line transect data for chaparral.

Species	Per cent of total vegetation touching transect line	Per cent of transect distance covered	Number of times appearing	Average Distance (m.) spread over transect line by individual plants
SCLEROPHYLLOUS SPECIES:				
Adenostoma fasciculatum	38.6	57.0	515	1.17
Ceanothus macrocarpus . . .	16.5	24.5	208	1.2
Ceanothus spinosus	0.38		8	0.76
Quercus dumosa	5.3	7.9	80	1.05
Rhus laurina	2.7	4.0	39	1.09
Rhus ovata	1.7		25	1.07
Photinia arbutifolia	0.77	. . . .	14	.85
Prunus ilicifolia.	2.2	. .	23	1.48
Cercocarpus betuloides . . .	0.93	.	17	.86
Arctostaphylos glandulosa . . .	2.97	. .	57	.82
Arctostaphylos glauca	1.97	. .	17	1.82
Ceanothus oliganthus. . .	1.34	. .	36	0.56
Total.	76.23	.	.	1.03 (Average)
NON-SCLEROPHYLLOUS SPECIES:				
Salvia mellifera	9.46	14.0	162	0.92
Salvia leucophylla. . . .	1.14		24	0.75
Eriogonum fasciculatum . . .	2.99	4.4	88	0.53
Erigonum cinereum	.52		9	0.92
Encelia californica. . .	.77	.	14	0.84
Lotus scoparius . .	.83		20	0.63
Isocoma veneta . .	.67	. .	26	0.41
Artemisia californica	.45	. . .	12	0.60
Total	16.83	. . .	. .	0.70 (Average)

Adenostoma fasciculatum was the outstanding species of this area, constituting 38.6 per cent of all the vegetation touching the transect line and covering 57 per cent of the distance measured. The species of second importance was *Ceanothus macrocarpus* which made up 16.5 per cent of the vegetation and covered about one-fourth of the line run, being, thus considerably less than half as extensive as Adenostoma. The species ranking third in abundance, *Salvia mellifera*, constituted 10 per cent of the vegetation but the figure gives the species more prominence than it deserves in undisturbed, mature, climax chaparral, because in such a community, the black

sage exists largely as impoverished specimens underneath the more characteristic chaparral shrubs where it is obviously not in control of the ground but yields evidence of a former successional stage in which it played a more important rôle.

In the summary of the transect data, Table 2, 20 species are listed. This includes all the species of any importance in this area, although a number of others were represented in insignificant amounts. Of the 20 species, 12 are classified as sclerophylls, and the others as non-sclerophylls. The distinction is based on the relative hardness and rigidity of the leaves although there are no definite standards for this character. Some of the species in the latter group, especially *Salvia mellifera* and *Eriogonum fasciculatum*, are somewhat sclerophyllous but they lack the degree of rigidity characteristic of the plants designated as sclerophylls.

The first column of the table gives the percentage of vegetation as based on the sum of all the distances of all the plants measured on the transect line. The second column gives the percentage of the transect distance, that is to say, the length of the transect line, for each species. In the third column are given the number of times the species appeared on the line, and in the fourth column the average distance that the individual plants of each species covered the transect line. This is not, be it noted, the diameter of the plant crown, because the line does not cross the center of the crown in most cases. The procedure does show, though, the relative sizes of the plant bodies. Thus the crowns of the non-sclerophylls are about one-third smaller than those of the sclerophylls.

The line transect method described above was used to determine the differences in composition and structure on the cardinal exposures. The four stations (8, 11, 12, and 13) utilized for this were all located near the top of a hill shown in the photograph (Fig. 2) and were all topographically very similar except as to the matter of the direction toward which the slope faced.

A summary of the results is given in Table 3, in which only the more important species are considered. *Adenostoma fasciculatum* was found to be the most abundant on all exposures. On the southerly-facing slopes it constituted 58.8 per cent of the vegetation touching the transects and covered over 70 per cent of the transect line. *Adenostoma* was over four times as abundant on this exposure as the species of second importance, *Ceanothus macrocarpus*. The more xeric conditions of the southerly slopes do not favor the broad-leaved species but seem to have little effect on *Adenostoma*. The easterly and westerly slopes were intermediate with reference to the abundance of *Adenostoma*, the westerly having a little more, thus indicating, perhaps, more xeric conditions.

. *Quercus dumosa* appears to be sensitive to slight differences in environ-

TABLE 3. Percentage of species touching line transects run on different exposures.

Species	North	East	South	West
Adenostoma fasciculatum	24.2	40.0	58.8	47.5
Ceanothus macrocarpus	23.2	25.3	14.5	9.2
Quercus dumosa	14.8	3.7	0.5	0.0
Rhus laurina	0.3	0.0	4.6	4.3
Rhus ovata	3.1	0.0	0.0	4.8
Arctostaphylos glandulosa	9.0	0.0	0.0	0.0
Arctostaphylos glauca	4.6	4.0	2.6	0.0
Salvia mellifera	1.1	24.4	8.5	27.4
Eriogonum fasciculatum	0.8	2.1	6.8	3.0
Overlap	58.0	34.8	30.9	37.4
All sclerophylls	95.5	73.5	83.0	68.0
Bare ground	7.2	5.5	12.1	4.3

ment. It was here almost wholly confined to the northerly exposures, where it constituted 14.8 per cent of the vegetation. There was a little on the easterly and practically none on the westerly or southerly exposures. *Arctostaphylos* was more common on the northerly than on the southerly slopes. *Salvia mellifera* was almost excluded from the northerly but was rather common on the other exposures.

Since the branches of neighboring shrubs are usually interlaced, a given area of ground is often covered by more than one plant and species. The extent of this double or triple covering is indicated in Table 3 by the term "overlap." This was 30.9 on the southerly exposures, and 58 per cent, or nearly two times as much on the northerly ones, with the easterly and westerly exposures intermediate.

In spite of the marked overlap some bare ground is usually encountered in traversing chaparral areas. This has been averaged for the different exposures, the southerly ones exhibiting the largest amount, namely, 12.1 per cent.

The dominance of broad-sclerophyll vegetation, including the one narrow-sclerophyll, *Adenostoma*, is very obvious. This type of vegetation ranged from 68 per cent on westerly slopes to 95 per cent on the northerly ones.

THE ENVIRONMENT

PRECIPITATION

The rainfall data obtained in this investigation are supplemented by records of other agencies, namely, the Los Angeles station of the United States Weather Bureau, the Los Angeles County Forestry Department, and the Los Angeles County Flood Control District. The diagrams in Figure 11 are based on the records of the U. S. Weather Bureau at Los Angeles. The top diagram shows the average monthly rainfall for this station for a period of over half a century. The middle diagram is for the single season of

1931-1932, the period during which weekly visits were made to all the stations of the present investigation. At the bottom is shown the season 1932-1933, the second year of this investigation.

It may be noted that the season 1931-1932 approached the theoretical average year about as closely as any one year is likely to do, in that the total was only slightly above normal and in that the important rains began in November and continued for several months. The most noticeable difference between this particular year and the average is the sudden ending of substantial rainfall with the end of February. The precipitation for the second year of the investigation was markedly different from the average in both amount and distribution, although it is not at all unusual for well over half of the annual rainfall to occur during a single month, as was the case in 1932-1933. Thus the general precipitation conditions during the course of the field work herein reported were not unusual.

The total rainfall for the year 1931-1932 for a number of locations in and near the area investigated is presented in Table 4. Some of these stations were near the ocean at the southern base of the range; some at the edge of the San Fernando Valley at the northern base; and others at various elevations within the mountains proper. Contrary to what might be expected, the rainfall near the ocean was considerably less than farther inland. For this one season it was more than 20 per cent greater at the northerly base of the mountains than it was at the southerly base, near the

TABLE 4. Total annual precipitation for the season of 1931-1932 for several stations in or near the central portion of the Santa Monica Mountains.

Station	Elevation	Precipitation
Near ocean at the south base of the mountains:	*Feet*	*Inches*
Mouth of Topanga Canyon[1]	85	19.55
Bel Air Bay Club...	90	13.52
Average........	...	16.53
Within the mountainous area:		
Malibu Headquarters...	747	28.23
Saddle Peak Road[1]	2200	30.17
Crag's Country Club	600	25.23
West Saddle Peak.	970	25.61
Topanga Summit..........	1560	21.08
Average		26.06
Near San Fernando Valley at north base of the mountains:		
Girard	892	18.09
Calabasas.....	950	19.68
Adohr Dairy..........	815	19.58
Average	....	19.11

[1]Data for these stations taken from original records of this investigation. Data for all other stations taken from records of the Los Angeles County Flood Control District.

JUL	AUG	SEP	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUN	
54 YR. AV. 14.96												1877 1931
.01	.03	.16	.65	1.18	2.56	3.06	2.98	2.78	1.03	.45	.07	
TOTAL 16.95												1931 1932
.00	.02	.24	.06	1.95	5.95	2.94	5.33	.01	.30	.02	.13	
TOTAL 11.88												1932 1933
.00	.00	.14	.08	.00	1.77	8.46	.00	.19	.56	.21	.47	
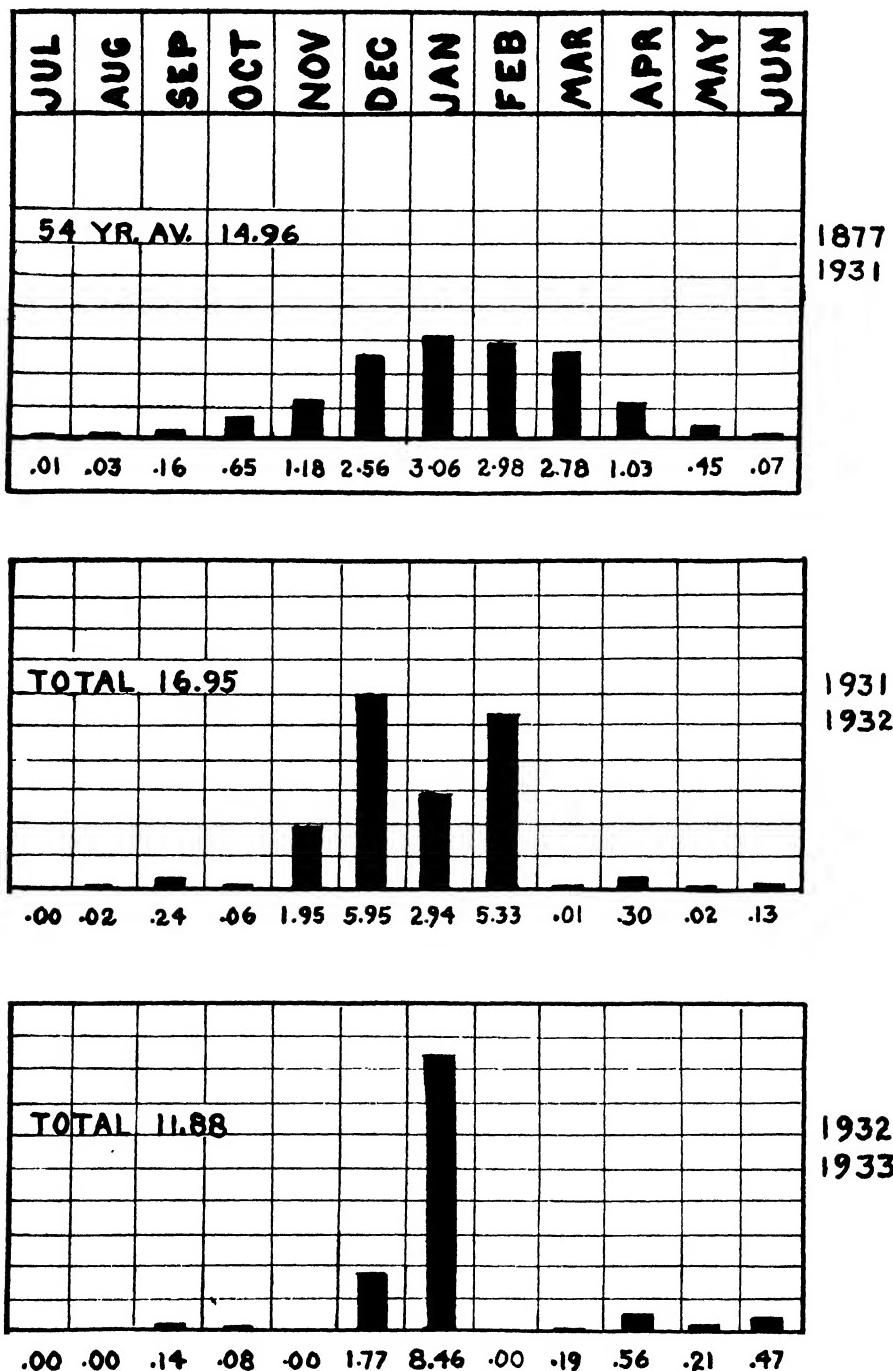
FIG. 11. Monthly distribution of rainfall at Los Angeles, California.

ocean. The variation among the mountain locations was considerable. For instance, Crag's Country Club, with an altitude of only 600 feet, had practically the same amount as the stations located at altitudes three or four times higher, but Topanga summit, with an elevation of 1,560 feet, located in the same canyon as Malibu Headquarters with an elevation of 747 feet, had considerably less rainfall than the latter station. It would appear from these facts that altitude is of less importance than distance from the ocean in influencing the amount of rain. The smaller amount near the ocean doubtless explains in part the more xeric character of the coastal sagebrush located there.

The direction in which a slope faces has considerable influence on the amount of rainfall received. In the Santa Monica Mountains, for the season of 1931-1932, the combined northerly and easterly slopes had about 20 per cent more than the southerly and westerly ones. A summary of results of the heavy rains is given in Table 5. The measurements were made by 3-inch U. S. Weather Bureau type rain gauges placed at Stations 8, 11, 12, and 13, all of which were located at about the same level on the hill shown in Figure 2. The differences in rainfall on the several exposures doubtless contribute considerably to the differences in vegetation, as previously described.

TABLE 5. Comparison of rainfall on different exposures during certain periods of heavy rainfall

Period	Northerly	Easterly	Southerly	Westerly
	Inches	Inches	Inches	Inches
January 30 – February 6, 1932....	5.22	5.46	4.41	4.00
February 6 - February 13, 1932	5.60	6.05	5.05	5.18
February 13 -- February 20, 1932.. .	1.32	1.47	1.39	1.34
January 15 – February 13, 1933....	14.20	14.85	11.64	11.96
Total	26.34	27.81	22.49	22.48

Some rainfall interception data were yielded by gauges placed under the foliage of certain species, all of which were located near station V. The results are summarized in Table 6 for three species, namely, *Adenostoma fasciculatum*, *Ceanothus macrocarpus*, and *Arctostaphylos glandulosa*, and show that 70, 66, and 57 per cent, respectively, of the rain passed through the leafy crowns of the plants. The average of intercepted rainfall for all three species was about 35 per cent. Some of this reached the soil by way of stems and trunks and the balance was returned to the air by direct evaporation. For the light rains at the beginning and end of the wet season, such interception is an important source of loss. It is interesting to note that the species with the smaller leaves intercepted less rain than those with larger leaves. This may explain in part the greater success of the narrow-

TABLE 6. Rainfall in the open and under the foliage of nearby chaparral shrubs, 1931-1932.

Date	In the open	Under Adenostoma	Under Ceanothus	Under Arctostaphylos
	Inches	Inches	Inches	Inches
September 26.............	.05	.03	.03	.01
October 3.....	.13	.04	.07	.05
October 24.............	.23	.10	.13	.12
November 21.............	1.25	.86	.85	.75
November 28.............	2.97	2.83	2.07	1.53
December 12.............	1.87	1.54	1.46	1.30
December 19.........	1.15	1.13	.90	.94
December 26.............	4.00	2.15	2.56	2.22
January 2.............	4.90	2.88	2.98	2.64
Total.............	16.55	11.56	11.05	9.56
Per cent passing through plant...	....	70.00	66.00	57.00

leaved *Adenostoma*, especially on the drier southerly exposures where it is more abundant than on other slopes.

SOIL MOISTURE

Samples of the soil for moisture determinations were cut from the walls of freshly dug trenches at all stations, on the occasion of each weekly visit. In nearly all cases samples were taken at two levels, namely, 10 cm. (surface) and 30 cm. (sub-surface), and at Station 8, where the soil was deeper, they were also taken at depths of 60 and 100 cm. The samples were dried in an electric oven at a temperature of 110° C. for a period of 48 hours. Weighings were in centigrams and the percentages of moisture calculated on the basis of oven-dry soil.

In order to get accurate information as to the capacity of these soils to retain moisture, and the amount of water readily available to the vegetation, determinations were made of both the moisture equivalents and the permanent wilting percentages.[1] The moisture equivalents were determined with a centrifuge according to the method of Briggs and Shantz (1912) and the results were used for the indirect calculation of the wilting coefficient. For the direct calculation of the permanent wilting percentages a slight modification of the Veihmeyer method was used. In this, dwarf sunflower seedlings were grown in glass tumblers having tin lids with small holes for the stems of the plants, and the moisture content was determined when the plants attained the permanent wilting point. The direct determinations were used as the basis of the wilting coefficient graphs in Figures 12 and 17, as the direct method has been found to be more accurate (Veihmeyer
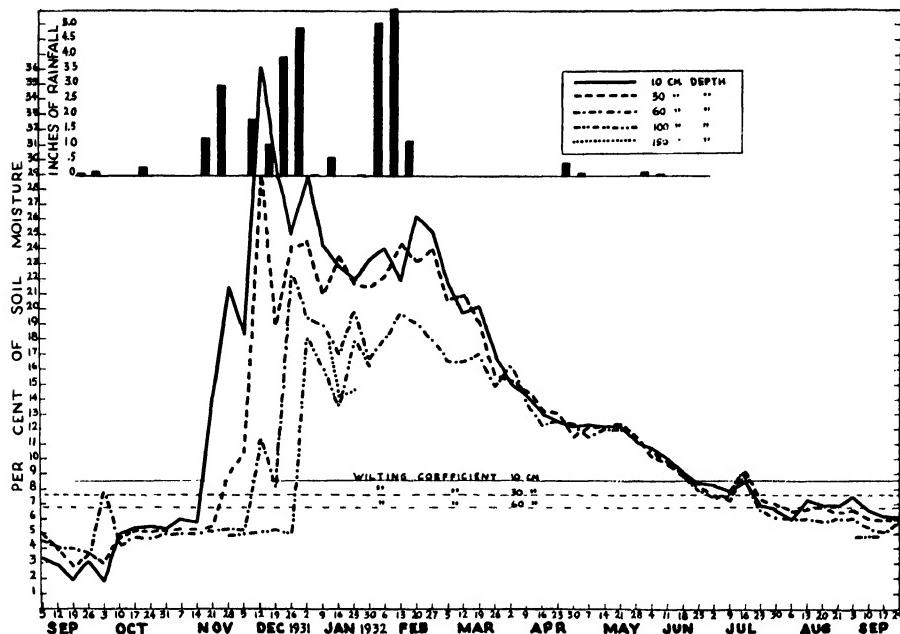
FIG. 12. Seasonal march of soil moisture at various depths, and other conditions in the chaparral. All data are for station 8, a northerly exposure at an elevation of about 2,300 feet.

and Hendrickson, 1928). The moisture equivalents and wilting percentages, like other edaphic conditions, were found to vary considerably, even within small areas where the vegetation was of fairly uniform character.

SEASONAL MARCH AND PENETRATION

The relations between precipitation, seasonal march, and penetration of soil moisture, and other features of soil moisture are shown in Figure 12. The graphs are plotted by weeks for a period of 13 months. All the graphs are for a single station (Sta. 8), but it is believed that this station represents fairly well the characteristic unburned chaparral of the area. The wilting coefficients for three soil levels are shown by horizontal lines.

Noticeable features are the extremely low content of moisture (3-5 per cent) in the soil during the dry summer months and the sudden increase (up to 30 per cent) in the surface level following the first substantial winter rains in November. The almost weekly rains maintained the moisture at somewhere near its field capacity during January and February.

The light rains at the beginning and end of the wet season made but very little change in the moisture content of the soil. The ineffectiveness of these first rains is shown by comparing the soil moisture graphs with the wilting coefficients. Although nearly half an inch of rain fell before the November storms, it did not raise the soil moisture above the wilting

coefficient, even at the 10 cm. depth, and the moisture from these rains did not, therefore, become available to the plants. Much of the light rains is intercepted by the vegetation and the layer of litter and humus material on the surface, and returned to the atmosphere by evaporation.

The slowness of the soil moisture below the 10 cm. depth to increase after the first heavy rains is significant. At the 30 cm. depth soil moisture rose a little during the first and second week following the rise at the 10 cm. depth but did not reach its field capacity until four weeks after the advent of the wet season. The soil at 60 cm. depth did not show any large increase in the moisture content until five weeks, and at the 100 cm. depth it remained as dry as in mid-summer until six weeks after the first heavy rains of the wet season. By the seventh week the water reached the 150 cm. level.

From these data it is apparent that, for the first meter of soil, even though the rains were heavy and frequent, water moved downward slowly, at the rate of only about 17 cm. per week. In coarser soil, penetration would be more rapid. The delay in the increase of the soil moisture in the lower strata means that, for the deeper roots, the dry season is some weeks longer, and the wet, or growing, season correspondingly shorter than for the surface layers. Cooper (1922, p. 46), who also observed the slow penetration of rain water, believed it was due to the air-filled condition of the soil.

A study of the intersection of the soil moisture graphs with the wilting coefficient lines shows that for roots more than one meter below the surface, there was no supply of readily available water until the first week in January, although heavy rains began about the middle of November and continued almost weekly. In ordinary situations in this chaparral most of the roots appeared to be near the surface, probably less than half a meter, and the plants had plenty of water for growth after the first ample rains. No evidence was found to show that root systems characteristically were especially extensive or deeply penetrating except where soil conditions were unusually inhospitable.

In contrast to the divergence of the graphs during the early part of the wet season, indicating wide differences in moisture content of the soil at the different depths, is the convergence of the graphs a few weeks after the last heavy rains of February, indicating uniformity of soil moisture at the several levels during the period when the soil was losing moisture most rapidly and when vegetative activity appeared to be at its highest rate. Apparently the plant roots absorbed moisture from each of these levels at about the same rate. There seemed to be but very little loss of water at this station (a northerly exposure) by direct evaporation from the surface of the ground, since the graph for the 10 cm. depth shows about the same

moisture content near the surface as at the deeper levels. This was probably due to retardation of surface evaporation by shade and ground litter.

During several months of the dry season, July to the middle of November, the moisture in the soil at the station being considered (Sta. 8) was below the wilting coefficient and the plants were. therefore, unable to get enough water for normal activities and were practically in a state of dormancy. During the 13 months considered here, soil moisture did not rise above the permanent wilting percentage until the latter half of November, and then at the 10 cm. depth only. The soil moisture at the 10 cm. depth dropped below the wilting coefficient in June, and at the 30 cm. and 60 cm. levels in the latter part of July. Thus for a period of about eight and a half months the plants were able to get water from at least one soil level. However, as will be pointed out later, another condition, namely, unfavorable temperature, was operative to prevent growth during the early part of this period.

The graphs in Figure 12 show a difference between the moisture content of the soil in September 1931 and September 1932. The average for the latter year was about 3 per cent higher than for the former year. In all probability this was due to the fact that the season previous to 1931 was below normal in rainfall whereas September 1932 followed a season above normal. These results are very similar to those obtained by Cooper (1922, p. 50) in the chaparral near Palo Alto, California, where the soil moisture content during the critical period following a season of deficient rainfall was very perceptibly lower than it was following a winter of abundant rain. The matter is of considerable significance because this initial moisture content determines how much water must enter the ground before the soil moisture is raised above the wilting coefficient and water becomes available for growth.

A comparison was made of the moisture content of the soil at Station 3. representing an area on which the chaparral had been recently burned, and at Station 4. located nearby in characteristic unburned chaparral. Both stations had southerly exposures. On the burned area the shrubs were sprouting from the root crowns, but much of the ground surface was bare, except during March and April when it was covered with a rather dense growth of herbaceous species. The results showed the moisture in the surface soil, 10 cm. level, varied approximately the same at both stations; in each case it dropped below the permanent wilting percentage in May. This depletion was due in part, especially on the burned area, to direct surface evaporation. At the 30 cm. level, however, the moisture situation was different at these two stations. On the unburned area, the soil moisture varied about as described for Station 8 above, dropping below its permanent wilting percentage near the end of July. At the 30 cm. depth on the

recently burned area, however, the moisture did not drop below its permanent wilting percentage at all, and averaged approximately 6 per cent higher than at Station 4 throughout the dry summer months, and had readily available water during this period. Apparently direct evaporation from the ground surface had little effect at this depth and the demands of the two-year-old shoots were not great enough to reduce the moisture to the permanent wilting percentage of the soil.

EVAPORATION

For the study of evaporation, there was set up at each station a battery of two or three Livingston white, spherical, porous cup atmometers equipped with the Livingston-Thone mercury-wool rain-correcting valves at the lower ends of the reservoir supply tubes in bottles of 1,000 cc. capacity. The porous cups, which were supported about 30 cm. above the ground surface, were cleaned weekly during the first year and restandardized at intervals of two or three months during the entire two-year period of investigation. All readings were corrected by the cup coefficients to the usual Livingston standard.

The atmometers were read weekly for 56 consecutive weeks, after which readings were made at four-week intervals to the end of the 104th week. The unbroken record of station readings for the entire period is probably rather remarkable in view of the number of instruments in service and the likelihood of disturbances by animals, man, and other agents. Some annoyance was caused by ants crawling through the air vent pipe, and, in a few cases during the second summer, by the growth of an unicellular green alga inside the glass reservoir supply tubes, but accuracy of the readings was probably not affected. A few of the cups were broken by the freezing of the contained water, but never all those at any one station, so that there was invariably at least one apparently valid reading at each station.

The coefficients of the cups changed but little during the progress of the work. Of the 32 new atmometer cups originally placed in service, 12, or 37.5 per cent, had undergone no change in their coefficients at the end of the first year, and eight, or 25 per cent, of them remained unchanged at the end of the second year. Individual cups were not in continuous use because of the periodic restandardizations.

SEASONAL MARCH

The most noticeable feature of the evaporation was its variability, the weekly readings usually showing a sharp rise or fall. In but a few cases only did the average daily evaporation for two consecutive weeks remain about the same for any one station, except at Station 1 which was markedly influenced by the proximity of the ocean.
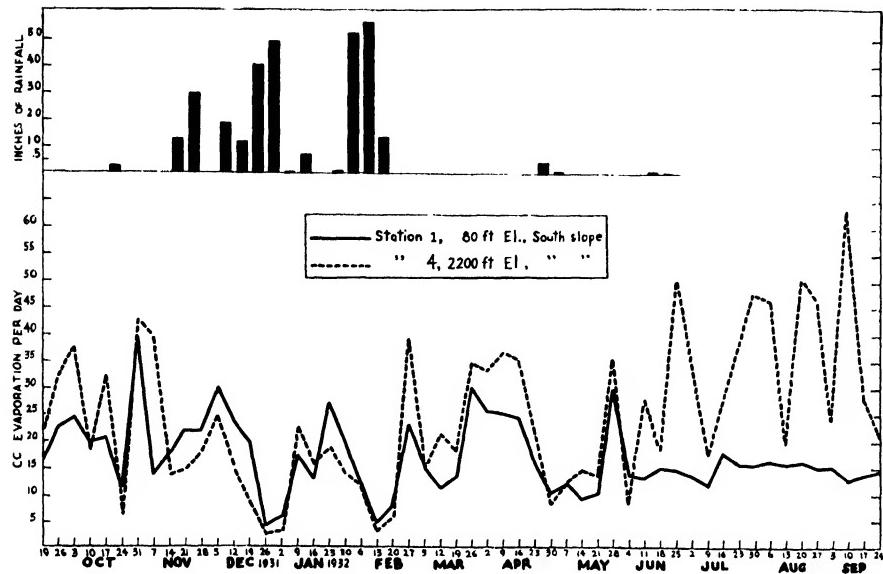
Fig. 13. Seasonal march of evaporation near the ocean and at an elevation of 2,200 feet.

.   The quality of weekly evaporation rates in all seasons is shown by the graphs for two stations, namely, 1 and 4, in Figure 13. Station 4, located at an altitude of a little over 2,000 feet and several miles from the ocean, is believed to represent faithfully the characteristic chaparral of this area. Fluctuations in evaporation at all stations, except those close to the ocean, were similar to those at this one.

In the seasonal march of evaporation, as indicated by the graph for Station 4, peaks showing average daily evaporation of 35 cc. or more appeared eight times, once in October, once in February, and six times in the six months April to September. Of these peaks, two remained as such for two consecutive weeks, and one for four consecutive weeks, March 26 to April 16, the period of most rapid depletion of soil moisture. Extremes of low weekly evaporation rates occurred with somewhat less frequency. At only five points did the evaporation drop to a daily average of 10 cc. or less. These low points were most prominent in the wet months of December and February. The marked rise in January coincided with a period of low precipitation and the decided fall in May was related to the light rains of that time.

The seasonal tendencies of certain stations for both years of the investigation are tabulated in Table 7. The stations averaged together represent this chaparral well and have unbroken and complete records of readings for the entire period under discussion. The daily mean for the entire two years was approximately 25 cc. As would be expected, the evapora-

tion rates were lowest in winter and highest in summer. The monthly averages showed February to be the lowest month, with December and January but very little higher, and August the highest month with July and September almost as high. The single month with the lowest rate was December, 1931, with a daily average of 12.9 cc., and the single month with the highest rate was September, 1932, with a daily average of 37.6 cc.

TABLE 7. Tendencies in evaporation.

	Year 1931-32. Average of four stations (2, 4, 5, 8,)		Year 1932-33. Average of two stations (8, 15)		Average of both years	
	Total	Average daily	Total	Average daily	Total	Average daily
			cc. of water evaporated			
October	762.9	24.6	914.3	29.5	838.6	27.0
November	601.0	20.3	1020.4	34.0	810.7	27.0
December	401.8	12.9	695.4	22.4	548.6	17.7
Total	1765.7	19.2	2630.1	28.6	2197.9	23.9
January	522.1	16.8	544.5	17.5	533.3	17.8
February	399.1	13.2	589.5	21.0	494.3	17.3
March	729.2	23.5	783.0	25.3	756.1	24.4
Total	1650.4	18.1	1917.0	21.3	1783.7	19.6
April	753.0	25.1	803.0	26.8	778.0	25.9
May	516.5	16.6	699.0	25.6	607.7	19.6
June	703.2	23.4	838.0	28.0	770.6	25.7
Total	1972.7	21.7	2340.0	25.7	2156.3	23.7
July	830.5	26.8	1155.0	37.2	992.7	32.0
August	975.0	31.4	1031.2	34.5	1003.1	31.2
September	824.1	27.5	1052.0	37.6	938.1	31.2
Total	2629.6	28.6	3238.2	35.2	2933.9	31.9
Year	8018.4	21.9	10125.3	27.7	9071.8	24.8

For weekly periods, the lowest evaporation rate was at Station 6, where the average daily evaporation for the week of December 26 to January 2, 1931-1932, was 1.9 cc. The highest weekly rate for atmometers placed with their cups 30 cm. above the ground surface, was at Station 12, a westerly exposure at an elevation of 2,375 feet, where the average daily evaporation was 79.5 cc. for the week of September 3-10, 1932. At Station 13, a southerly exposure where evaporation was measured at the top of the vegetation, that is, 2 m. above the ground, a daily average of 90 cc. was recorded for the same week.

The evaporation conditions during the second year of the investigation were in some respects markedly different from those of the first. The evap-

oration in every month was higher during the second year than in the corresponding month of the first year, being greater by a daily average of 10 cc. or more for the months of November, December, July, and September. The daily average for the entire year, 1932-1933, was 5.8 cc. more than for the year 1931-1932. Thus evaporation, like precipitation, may vary considerably from year to year, the greater evaporation occurring during years of lower precipitation, thus increasing the unfavorability of the chaparral environment.

INFLUENCE OF THE OCEAN

A comparison of the two graphs in Figure 13 shows that the ocean had a very marked equalizing effect upon evaporation in the nearby vegetation. At Station 1, the sea-level station, evaporation during most of the year fluctuated in the same direction as it did at Station 4, representing the characteristic chaparral of higher elevations located several miles inland, but did not attain either such high or low extremes.

The most striking feature indicated in Figure 13, however, was the difference in evaporation at these two stations during the four summer months, June to September, 1932. During this period evaporation at the higher elevation station varied from an extreme low of 9 cc. as a daily average to a high rate of 64 cc., and the fluctuations were the most marked of any time of the year. Out of the 16 weeks of this period, evaporation was above a daily average of 45 cc. for six weeks and below 25 cc. for five weeks. On five occasions two consecutive weeks had a difference of 25 cc. or more as a daily average, one of these being a difference of 40 cc. In striking contrast to this was the low and almost uniform evaporation at the station near the ocean. The average daily evaporation for the entire period was only about 15 cc. and the variation from the lowest to the highest point was only 5 cc. Station 14, which was established February 20, 1932, about a quarter of a mile farther up the canyon from Station 1, and as a check upon this lower station, showed the same uniformity but ran consistently lower by a daily average of from 1 to 3 cc.

The records for Station 2, located about two miles from the ocean and at a well protected place within Topanga Canyon, still showed the influence of the ocean, though to a considerably lessened extent. The fluctuations at this "canyon" station were greater and both the high and low points were farther from the average than was the case closer to the ocean. These fluctuations, however, were by no means as marked as those described above for Station 4, at the higher elevation.

The indications are that conditions of low and uniform evaporation are found only on areas close to the ocean and in the canyons and deep ravines that extend a very few miles inland, and are not representative of evaporation in general in the chaparral of a coastal mountain range. All

of the stations located out of the canyon, and at an altitude of about 2,000 feet, exhibited comparatively high and much more variable evaporation rates.

INFLUENCE OF FIRE

It might be supposed that evaporation on recently burned areas, where much of the ground is bare and the atmometers were placed where the sun strikes them directly, would be considerably higher at all times than in a dense chaparral thicket where the atmometers are shaded nearly all the time. The differences found in this investigation, however, were not very marked. The fluctuations at Station 3, located on an area that had been burned one year previous to the beginning of the instrumentation, coincided with those in a nearby unburned chaparral with a similar southerly exposure, the amount of evaporation on the burned area being greater during most of the time but only by a little over 10 per cent for the year. The evaporation on the burned area was about 18 per cent greater than at Station 5, which had a northerly exposure.

The evaporation rate on the burned area was actually less than that on the nearby unburned area for a period of seven weeks, February 27 to April 9, 1932, with the exception of a single week. This period followed the end of the interval of heavy rains and coincided with the period of most rapid vegetative activity and depletion of soil moisture. At this time a rather rank growth of grasses and other herbs covered much of the ground of the burned area. The decreased evaporation rate at Station 3 was doubtless due largely to increased humidity caused by transpiration from the herbaceous vegetation surrounding the atmometers and also to breezes bearing the moisture of transpiration from the extensive herbage-covered slopes of the burned area. The evaporation rate at Station 3 might have been somewhat higher had the station been located farther from the edge of the unburned chaparral, this distance being about 25 feet. No evidence in favor of this possibility was noted, however, in the readings from Station 9, a second "burned chaparral" station established April 16, 1932, and located well removed from unburned vegetation. The indications were that the destruction of chaparral by burning did not seriously increase the intensity of evaporation.

INFLUENCE OF EXPOSURE

From the standpoint of evaporation, growth conditions are most favorable on north-facing slopes and least so on southerly exposures, this being especially the case during the critical months of the summer. The influences of slope exposure are illustrated graphically in Figure 14 for the six months, April-September, 1932. The graphs representing the northerly, easterly, westerly, and southerly exposures are based on the records of
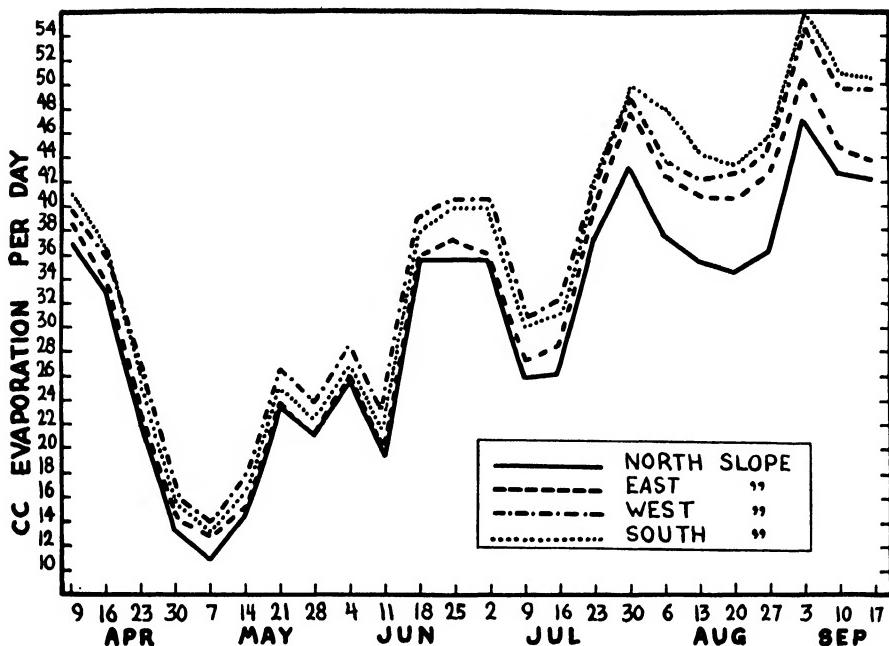
FIG. 14. The influence of slope exposure on evaporation.

Stations 8, 9, 12, and 13, respectively. All of these stations had approximately the same elevation of about 2,350 feet, and were located on different sides of the same hill (Fig. 2). None was protected by neighboring prominences, so that the differences in evaporation were apparently due entirely to the direction in which the slopes faced. In constructing the chart all the graphs were smoothed out somewhat by averaging three consecutive readings, thus: 1st, 2nd, and 3rd; 2nd, 3rd, and 4th; 3rd, 4th, and 5th; and so on. This simplifies the graphs and makes clearer those general tendencies which are most important in making such comparisons than are the absolute amounts of evaporation.

For the period plotted, the evaporation rate on the southerly exposure was consistently the highest and that on the northerly exposure the lowest, while on the westerly exposure evaporations were somewhat higher than on the easterly. The difference in the evaporation rates on the southerly and northerly exposures during the periods of low evaporation was not marked, being only about 2 or 3 cc. per day. The graphs are separated much more widely during the drier months of the summer. Computations show that for the three months, April to June, evaporation on the southerly exposure was about 10 per cent greater than on the northerly, but during the three months, July to September, it was about 20 per cent greater on the southerly.

EVAPORATION AT DIFFERENT LEVELS

For the purpose of comparing the evaporation rates at different levels in the chaparral, a standard for supporting atmometers above the ground was erected at Station 13, a southerly exposure with an elevation of 2,350 feet. One pair of atmometers was supported at the top of the vegetation, 2 m. above the ground where they were unshaded at all times; a second pair near the middle of the foliage mass, 1 m. above the ground; and a third pair was placed on the ground in the same way as at all other stations. The apparatus is shown in Figure 10. The vegetation at this station was about 60 per cent *Adenostoma fasciculatum*.

The highest rate of evaporation was found at the top of the vegetation and the lowest at the middle level. The readings of the ground atmometers were consistently higher than those of the one-meter level in spite of denser shade at the ground level. This was doubtless due in part to greater amounts of moisture transpired at the middle level, and, in part, to the fact that temperature at the ground level was slightly higher. From the summarization of Table 8, it is apparent that, taking the evaporation at the top of the vegetation as 100, the ratios of the top, middle, and ground levels were 100:83:86, respectively.

It might be supposed that the higher evaporation at the top of the vegetation was due to higher temperatures, since the atmometers here were unshaded. Such, however, was not the case, as a series of temperature readings showed the temperature at the top to be decidedly lower, by an average of about 3° C., than at the lower levels. The temperature at the ground level averaged about 1° higher than at the middle level. The temperatures were taken at various times during July and August and each figure for temperature given in Table 8 is an average of over twenty readings. No exceptions to the relative order of temperatures given were recorded, and it is therefore believed that the relation of temperature at different levels as stated, may be a general one for these summer months.

In view of the lower temperatures at the top of this vegetation it is not certain why the evaporation there should be higher by about 20 per cent.

TABLE 8. Evaporation rates and temperatures at different levels at Station 13 for a period of twenty-eight weeks in the spring and summer, April 9 to September 24, 1932.

| Height above ground	Evaporation in cc.		Evaporation ratio	Temperature, degr. C. Av. of readings	Temperature ratio
	Total for period	Average daily			
Surface............	6857.1	35.0	86.	35.2	100.0
1 meter............	6603.3	33.7	83.	34.2	97.2
2 meters...........	7946.4	40.5	100.	31.9	90.7

FIG. 15. Evaporation in the chaparral at different levels above the ground. All data for Station 13, a southerly exposure at an elevation of about 2,350 feet.

Solar radiation is probably unimportant since white cup atmometers were used. Air movement probably accounts for much of the increase. Wind movement is less in the vegetation than over its top, and the vapor resulting from transpiration is not removed so readily, thus tending to increase the humidity and decrease the evaporation within the foliage mass. The main features of evaporation at different levels are shown in Figure 15.

EVAPORATION AND RADIATION

For a period of six weeks, February 11 to May 25, 1932, two black cup atmometers were maintained close to the two white ones at Station 9, in the recently burned area. During the six weeks period following this, April 1 to May 6, the black cup atmometers were placed beside the white ones at Station 8, in characteristic unburned chaparral on a northerly slope. This apparatus constituted a so-called radio-atmometer, for the approximate measure of the influence on evaporation of the impinging radiation from sun, sky, and earth. The greater evaporation from the black cups is due chiefly to the drying influence of radiation, the chief component of which is direct sunshine. The difference in the corrected readings of the black and white cups is, therefore, a measure of the effective intensity of radiation (Livingston, 1935, p. 469).

At Station 9 the evaporation as measured by the black cups was about 19 cc. per day more than that measured by the white cups, an average in-

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FIG. 16. Soil temperatures at stations representing different conditions in the chaparral.

INTERRELATION OF FACTORS

GROWING SEASON

In a region with winters so mild that temperatures seldom reach the freezing point it might be conjectured that the growing season for native vegetation would coincide with the period during which water is readily available. If this were true, the growing season could be calculated theoretically from soil moisture and permanent wilting percentage data. It was previously pointed out that water was readily available from the middle of November to the end of July, a period of about eight and a half months or two-thirds of the year. Noticeable activity on the part of the plants, however, was restricted to a much shorter period. There was practically no external evidence of plant activity during November and December, 1931, and in January, 1932, the only evidence of growth was the flowering of a very few species.' Since these are the coldest months, it is apparent that the temperatures are low enough to greatly restrict the absorption of water by roots, and other plant activities, so that growth could not continue and the real growing season does not, therefore, start until both soil and air tempera-

tures have risen to a favorable minimum. This is in accord with the conclusions of Maximov (1929, p. 83) in his discussion of the influences of temperature on water supply.

In order to procure more exact evidence as to the beginning, height, and end of the growing season than could be obtained from phenological observations, a series of measurements of the increase in length of certain stems was made. In doing this, three or more stems of normal appearance on plants of the chosen species were marked near the tip with waterproof ink, and measurements of any increase in length were made on the occasion of the regular weekly visit to the stations. Numerous accidents happened to the marked stems but enough of them remained intact to give significant information. Most of these were on stump sprouts at the edge of the burned area near Stations 3 and 4 where growth conditions were doubtless better than in the unburned chaparral. The graph for stem elongation shown in Figure 17 represents the average weekly growth of three species, *Adenostoma fasciculatum*, *Rhus laurina*, and *Photinia arbutifolia*.

Inspection of the graph shows that a small amount of stem elongation growth occurred in the fall, about the latter part of November or early December. No further growth in length was recorded until the latter part of February when it began rather suddenly and continued until about the first of July. Following this, elongation decreased and ceased entirely about the middle of July. The most rapid growth occurred during the latter part of March and the first part of April.

During the second year of this investigation the measurements of stem elongation at Station 3 were repeated and additional stems representing the same and other species were measured at Stations 9, 14, and 15, the last two representing characteristic unburned chaparral. The average elongation of over 20 stems of five different species was just about the same as in the first season. The most noticeable difference was the fact that elongation persisted somewhat longer into the summer, due, no doubt, to the lateness of the spring rains.

These data are not intended to constitute a complete quantitative record of growths at the ends of the marked stems. They are employed here only for the clues they supply as to the salient features of the growing season. The weaknesses inherent in the method are recognized. The series of measurements might well have included a greater number of species from the unburned chaparral. Nevertheless, it is believed the results approximate fairly well the significant responses made by the plants to the growing conditions.

From a consideration of the observations made during the two years of this investigation, it may be concluded that the characteristic events of the ordinary growing season are about as follows. There is a short and relatively unimportant period of growth in the fall, after the advent of the

first rains and while temperatures are still favorable. This is followed by a
month or more of inactivity, due to low temperatures. The beginning of
flowering comes in January and continues in different species until mid-
summer. A period of rapid vegetative growth occurs in March and April
followed by a period of lowered growth rate in May and June. After this
vegetative activity diminishes and ceases entirely in July.

MOISTURE RATIO

Since moisture conditions constitute the critical feature of the chaparral
environment, it is desirable to use a single numerical value to express this
factor as comprehensively as possible. For this purpose various ratios may
be employed. A rainfall-evaporation ratio (R/E) has sometimes been used,
but this is not suitable for southern California on account of the peculiar
distribution of the precipitation, one in which most of the rain falls in a sin-
gle or a very few months, while in other months there is little or none.
Thus this ratio applied to the Santa Monica Mountains would indicate very
poor moisture conditions in March and April, a time when the plants are
actually making their most rapid growth.

An evaporation-soil moisture (E/SM) ratio, which brings together the
most important factors of both the atmosphere and soil, much more ade-
quately represents the favorability or unfavorability of growth conditions
in southern California. Shreve (1927, p. 409) employed this ratio in
Arizona and California. In the present investigation it was found that the
most favorable E/SM ratios, those of about 1.0, existed during December,
January and February, and that during March, April and May they averaged
about 2.2, being only slightly less favorable. In June and July the ratios,
averaging about 4.0, indicated severe moisture conditions, and in August
and September they showed extreme conditions, averaging about 5.5. The
highest ratio found was one of 7.0 in September. The E/SM ratios for the
second year of the investigation were remarkably similar to those of the
first, in spite of the fact that the precipitation was quite different.

THE RELATION OF FACTORS TO EACH OTHER AND TO THE GROWTH
OF STEMS IN LENGTH

For the purpose of presenting in conjunction those features of the en-
vironmental complex that have been considered, and to indicate something
of the relation of the environmental complex to chaparral, all the important
moisture factors for the year 1931-1932, including precipitation, soil mois-
ture, wilting coefficients, and evaporation, have been brought together, with
soil temperature and the growth of stems in length, in a single chart
(Fig. 17). Herein the data are plotted on a weekly basis for 56 consecutive
weeks. All of the data are based on averages of four selected stations,
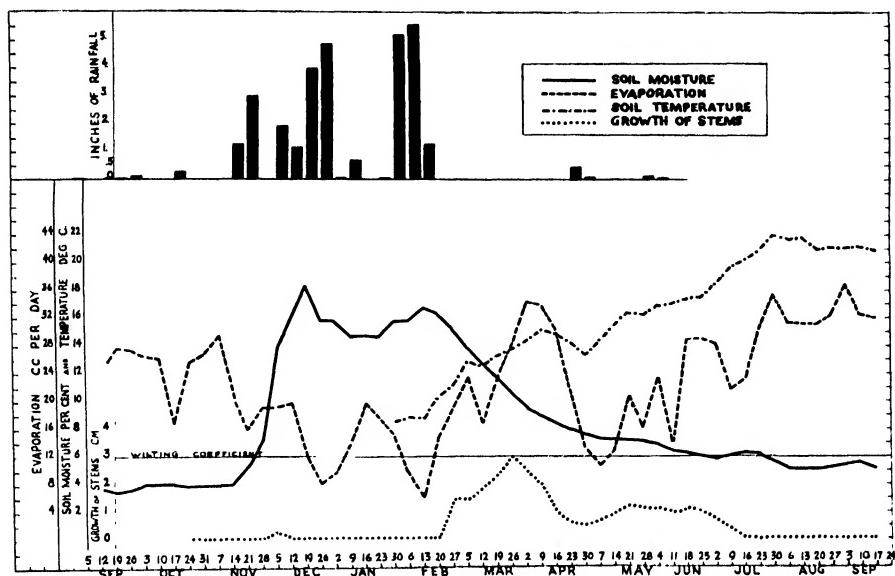
FIG. 17. Interrelations of the physical conditions in the chaparral habitat, and the growth of plants as represented by stem elongation. Each graph is somewhat smoothed and is plotted from data averaged for four stations.

numbers 2, 4, 5, and 8. Of these, two were northerly and two southerly exposures. Three of the stations were at elevations of a little over 2,000 feet, and the fourth was in a canyon at an elevation of 400 feet. It is believed that this selection faithfully represents general conditions in the chaparral of the Santa Monica Mountains. All of the graphs in the figure have been smoothed out by the method described on page 439 in order that the major tendencies might be more apparent.

Some of the features shown in Figure 17, such as the relation between precipitation and soil moisture, the rapid fluctuation of evaporation, and the increase in soil temperature, have been previously considered as they applied to certain individual stations. The limitation in the length of the growing season imposed by the availability of water is marked by the intersections of the soil moisture and wilting coefficient graphs. Thus it may be seen that, for the year 1931-1932, water was available from the latter part of November until the end of July, a period of about eight and one-half months. The figure shows that there was a striking lack of agreement between soil moisture and evaporation conditions in that, during much of the period when soil moisture was abundant, evaporation was very low, indicating that some of the factors influencing evaporation were not favorable to plant activity. Evaporation measurements express in large measure the effects of temperature, relative humidity, and wind. It is probable that temperature is the effective factor in restricting plant growth during periods of low evap-

oration, since the temperatures recorded for the period of plant inactivity studied were lower than those for any other time, whereas wind movement for this period was not unusual, and it is not probable that the comparatively high humidities inhibited growth. The soil temperature graph shows that the temperature of the soil increased rather steadily from about 8° C. in January to 22° C. in July. The upward trend of the soil temperature graph is rather similar to that of evaporation but it steadily diverges from that of soil moisture. It may be noticed that stem elongation did not begin until the temperature of the soil rose above 10° C.

The relations of the graph of stem elongation to those of the physical conditions are significant. The small amount of growth that occurred in early December, was after the first substantial rains and before evaporation dropped below 16 cc. per day. No further elongation of stems occurred until the end of February, when evaporation increased to more than 16 cc. per day. The temperature of the soil at this time, the latter part of February, had risen above 10° C. The average weekly elongation of stems of the selected plants was comparatively rapid for a period of eight weeks, February 27 to April 16, attaining a maximum of 3 cm. per week at the end of March. By the end of April, stem elongation had dropped to 0.5 cm. per week. Then it increased again to an approximate average of 1 cm. per week in May and June, after which it decreased, and in the early part of July ceased entirely.

All growth phenomena of plants are not, of course, represented in stem elongation. In the year 1932-1933 Arctostaphylos was in full bloom in January, seven or eight weeks before stems had begun to elongate, and *Rhus laurina* was still blooming in July a few weeks after stem growth had stopped. Nevertheless, the period of most rapid stem elongation doubtless indicates a time when the complex of environmental conditions is especially favorable for plant activity, and it may be when they average best for physiological processes.

During the period when stem elongation was most rapid, March and April, the evaporation and soil temperature conditions were moderate and the decreasing supply of soil moisture still averaged 5 or 6 per cent above the permanent wilting percentage. In April the soil moisture averaged about 2 per cent, and in May about 1 per cent, above the wilting coefficient. In July, when stem elongation stopped and the flowering of a few species was the only visible activity of the plants, soil moisture remained close to the wilting coefficient.

The relations between the fluctuations of the stem-elongation graph and the evaporation graph are curious. It is probably more than coincidence that most of the noticeable increases in elongation followed one or two weeks after a drop from a somewhat high to a moderate or medium weekly evap-

oration rate and, conversely, that the decreases in the elongation rate followed increases of the evaporation rate. The large decrease in the rate of stem elongation in April followed a rather sustained period of high evaporation, during which the average daily evaporation was 30 cc. or higher, and during which both soil moisture and soil temperature were favorable. During such a period of high evaporation it is likely that the loss of water from the plant due to rapid transpiration is so great as to interfere with the normal physiological processes of the plant and to retard its rate of growth.

During the succeeding year, 1932-1933, the chief relations just illustrated as existing between soil moisture, soil temperature, and stem elongation for 1931-1932, were found to prevail again, the differences being of minor importance. Somewhat more stem elongation occurred in the autumn of 1932 than in the previous year. This may have been due to the fact that the initial soil moisture content was about 2 per cent higher than at the beginning of the first year and consequently less rain was needed to bring it the wilting coefficient.

From a consideration of the correlations presented it appears that the most important conditions in the chaparral environment are the moisture relations, the effects of which are influenced somewhat by the low, but seldom freezing, temperatures of the winter months. The most critical period is the late summer, August and September, and that part of the autumn which precedes substantial rains. At this time the soil moisture is below the permanent wilting percentage and the high evaporation causes serious losses of water from plants.

Local variations in the physical conditions are caused by topographic features such as the proximity of the ocean, slope exposure, slope gradient, and altitude. The effects of these are reflected in minor changes in the structure of the vegetation, but the ecological type of chaparral is not markedly altered since it may be observed to spread in an almost unbroken mantle over the mountain complex. Occasionally, as at the bottom of a canyon or deep ravine, moisture conditions make possible the growth of trees, and here the chaparral gives way to the closely related broad-sclerophyll woodland. In other limited areas, as at the base of the mountains on either side of the range, there is not enough available water to support characteristic chaparral and the more xeric coastal sagebrush appears.

The advantages of the evergreen sclerophyll habit that is so characteristic of chaparral have been described by Schimper (1903, p. 513) and Cooper (1922, p. 66). The ever-present photosynthetic apparatus makes it possible for the plants to utilize warm periods in the winter and early spring months for food synthesis, when other plants have no leaves or are expending energy in making them. Thus an effective growth can be made

before the soil moisture drops below the permanent wilting percentage in the summer.

From the data obtained in this investigation, there is little reason to believe that shoot-growth activities during the winter months are important, but it is obvious that a vigorous flowering and vegetative activity starts without delay as soon as the temperatures of air and soil have risen above the minima necessary for these physiological processes. The sclerophyllous habit, which is chiefly due to the heavy layer of cutin, thick epidermis, and compact mesophyll, is an effective aid in conserving the scanty supplies of moisture during the critical period from August to October or November, so that, despite large transpiring surfaces, enough water is absorbed by the roots to maintain the necessary physiological processes at low rates.

The reason for the marked uniformity in size and general appearance of chaparral plants is not clear. Trees are doubtless excluded because of insufficient soil moisture, and smaller shrubs and herbs are probably kept out by the shade of the dense broad-evergreen leaves. In view of the taxonomic diversity of chaparral areas, however, more variation in the height of the shrubs might be expected. Wind, through its desiccating influence, may be a factor in preventing branches from growing more than slightly above the general level of the vegetation. Attention has been called to the fact that evaporation at the top of the vegetation on a southerly slope exposure was about 20 per cent greater on the average for a period of 28 weeks, April 9 to September 24, 1932, than it was at 1 m. lower, i. e., within the foliage mass. Thus a branch growing much above the general level of the vegetation would be subjected to the handicap of much greater desiccation and might not be able to continue its development. In the proximity of the beach, where vegetation is unprotected from the direct sweep of ocean winds, thickets, which may be composed of half a dozen species, are so even on the top as to give the appearance of having been artificially trimmed. Wind alone, however, does not appear to be an adequate explanation for the uniform heights of chaparral shrubs as they are found growing generally over wide areas embracing diverse situations.

SUMMARY

1. An intensive instrumental investigation during the two years 1931-1932 and 1932-1933 was made of the vegetation, chiefly chaparral, and the physical conditions, especially soil moisture and evaporation, of a representative area of the Santa Monica Mountains, California.

2. The flowering period of most chaparral species was of only a few weeks duration, but flowering activity continued among the various species for over half the year, the greatest wave of blossoming activity came in the latter part of March and in April.

3. *Adenostoma fasciculatum*, the most abundant species, was found to constitute 38.6 per cent of all the vegetation touching the line transects and to cover 57 per cent of the total distance of the transect lines run in various places. The species of second greatest abundance was *Ceanothus macrocarpus* which constituted 16.5 per cent of the vegetation and covered 24.5 per cent of the transect distance. *Salvia mellifera*, an important species in the coastal sagebrush, constituted 9.5 per cent of the vegetation, but the plants usually occurred underneath the taller sclerophyllous shrubs and were often not in control of the ground. In such situations this species is probably a remnant of a seral community that appeared after fire.

4. Southerly exposures were found to have nearly 60 per cent *Adenostoma fasciculatum*, but northerly ones only about 25 per cent. *Quercus dumosa* constituted about 15 per cent of the vegetation on northerly slopes, but very little of this species occurred on other exposures. The overlapping or interlacing of branches of chaparral shrubs was computed to be 58 per cent on northerly but only about 31 per cent on southerly exposures.

5. In this area more than 90 per cent of the rain normally falls during the six months, November to April, and the summer months are practically rainless. During the years of this investigation, it was found that the precipitation within the mountainous area was nearly 50 per cent greater than close to the ocean and that 20 per cent more rainfall was recorded on northerly and easterly exposures than on southerly and westerly ones. Measurements indicated that about one-third of the light rains of the early and late portions of the wet season was intercepted by the vegetation, the plants with larger broader leaves intercepting more than others. This may account in part for the greater success of the narrow-leaved *Adenostoma fasciculatum*.

6. Soil moisture was available to plants for a period of about eight and one-half months, November to July. Penetration in a fairly fine-textured soil was slow, six weeks being required for the moisture to reach a depth of 1 m. although substantial rains occurred almost weekly. After the end of the period of heavy rains, soil moisture decreased uniformly at all levels. On an area where the chaparral had been recently destroyed by fire, the water content at the 30 cm. level was above the permanent wilting percentage throughout the year, thus indicating that the vegetation is chiefly responsible for the depletion of soil moisture rather than direct surface evaporation.

7. Evaporation, as measured by Livingston white porous cup atmometers, was found to fluctuate greatly, the rate seldom remaining high or low for more than two consecutive weeks. The average rate for all seasons was 25 cc. per day. During the dry season the evaporation rates near the ground (30 cm. level) exceeded 50 cc. per day on a number of

occasions and attained an extreme high rate of nearly 80 cc. per day. The ratio of evaporation at the top of the vegetation (2 m. level), middle of foliage mass (1 m. level), and near the ground surface (30 cm. level) was 100 :83 :86. The considerably higher rate at the top of the vegetation is interesting in view of the fact that the temperatures there averaged about 3° C. lower during July and August. Evaporation on an unshaded recently burned area was found to be higher by 10 per cent than on characteristically unburned areas nearby.

8. On a recently burned area, evaporativity, as measured by Livingston black porous cup atmometers, was found to be 66 per cent greater than the evaporating power of the air as measured by the white porous cup atmometers, but in the shade of the characteristic chaparral on a northerly exposure the evaporativity was only 44 per cent greater.

9. Atmospheric moisture, as shown by determinations of the saturation deficit and relative humidity, varied rapidly from time to time and place to place. The average saturation deficit close to the ocean was 3.9 mm. for a number of readings made at various times throughout the year, but at elevations of about 2,000 feet and about three miles inland it was 10.5 mm., showing conditions considerably more than twice as arid. On the peaks, the relative humidity during the summer months averaged about 45 per cent as compared with 72 per cent in Topanga Canyon.

10. Soil temperatures at a depth of 10 cm. fluctuated considerably but there were no especially rapid changes at depths of 30 cm. and 60 cm. The deeper levels were very slightly warmer in winter and slightly colder in the summer than near the surface. At a depth of 30 cm. the temperature of the soil averaged less than 10° C. in February and between 18 and 28° C. in August and September. Air temperatures during the winter months occasionally dropped slightly below the freezing point for short periods.

11. The most active period of growth, as expressed by measurements of stem elongation, was March and early April when the soil contained an abundance of available water and the soil temperature was above 10° C. Stem elongation continued at decreasing rates through May and June and stopped entirely about the middle of July when soil moisture dropped below the permanent wilting percentage. A small amount of stem elongation took place in the autumn but none during the early portion of the winter when temperatures were low. There was fairly good correlation between stem elongation and an evaporation-soil moisture ratio (E/SM) in the latter, but not the earlier part of the growing season.

12. Wind may be a factor in causing the striking uniformity in the height of chaparral shrubs, in that it greatly increases the severity of evaporation just above the general level of the vegetation.

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THE ECOLOGY OF *PASSALUS CORNUTUS* FABRICIUS, A BEETLE WHICH LIVES IN ROTTING LOGS

By

A. S. PEARSE, MARGUERITE T. PATTERSON,
JOHN S. RANKIN, AND G. W. WHARTON

Duke University
Durham, N. C.

CONTENTS

THE ECOLOGY OF *PASSALUS CORNUTUS* FABRICIUS, A BEETLE WHICH LIVES IN ROTTING LOGS

INTRODUCTION

The beetles in the family Passalidae are of particular interest because they furnish examples of primitive societies. According to Wheeler (1928) there are social insects in six families of beetles. All these live in cavities in plant tissues. Wheeler characterizes a society as an "accumulative collectivity." Among such insects as termites there are extensive architectural accumulations and a complex system of castes. These have been made possible by social life. Termites "early resorted to a food-supply which was abundant and readily obtainable but not easily assimilable." Perhaps all social life among insects was at first associated with and made possible by such dependable sources of food as wood, and later evolved more elaborate social appurtenances in the way of polymorphism, trophyllaxis, mycetophagy, etc. Today termites are well organized in a ligneous environment, but beetles are just becoming established.

Passalid beetles are common throughout the warmer parts of both hemispheres. They were first studied extensively in Brazil by Ohaus (1899). A pair make rough galleries in damp rotten logs and live there with their progeny. The eggs are laid in a loose cluster and watched over by the parents. The adults and larvae both stridulate. The former produce squeaking sounds by rubbing the abdomen on the wings; the latter have a reduced pair of hind legs which they rub against the sides of the body. Stridulation serves to keep members of a colony together. Passalids show no castes; in fact, it is difficult or impossible to distinguish the sexes by external features.

It has been believed that the larvae of passalids require food which has been triturated and mixed with secretions produced by the parents. Like all social beetles, passalids depend on an abundant vegetable food and the parents care for the young to some extent. They avoid competition with other animals by utilizing foods which are indigestible for most other types. In rotting logs they also have the advantages of protection from enemies and a certain degree of thermal and hydric stability. Wood retains water, which has a high specific heat, and thus not only furnishes necessary moisture but prevents rapid temperature changes. Organic decay tends to keep a log warm when there are extremely low temperatures outside. Park (1935) has carried out extensive experiments to test the periods of rest and activity of *Passalus cornutus*. He kept the beetles in logs and subjected them to various external conditions of light and temperature. They were active as much during day as during night. In their relatively constant environment there was little or no diurnal periodicity.

The Duke Forest furnishes abundant material for the study of the activities of *Passalus cornutus*. Many rotting logs contain extensive galleries which are occupied by colonies. Oak and hickory logs are most often used as homes, but at times gum, dogwood, sourwood, and other woods are excavated. Rarely a pair may be found in a pine log. As many as ninety-odd passali were found in one large log. These were members of several colonies.

FIG. 1. *Passalus cornutus* Fabricius: dorsal view; X 3.6.

Beetles were studied during the years 1933, 1934, and 1935. In 1933 and 1934 routine monthly examinations were made during an entire year. Thanks are due to Miss Elizabeth Pearse and Mr. David Palmer who helped with routine observations and in the making of some of the drawings of parasites. Dr. C. F. Korstian identified all woods. Professor F. A. Wolf gave helpful advice at various times and Professor R. F. Poole furnished pure cultures

of three species of wood-rotting fungi. All work on foods was done by Mrs. Patterson and Rankin; that on parasites by Pearse and Wharton.

SEASONAL CYCLES

Though *Passalus cornutus* shows little or no diurnal periodicity, its breeding activities are definitely correlated with changing seasons in the Duke Forest. In the middle of April (1934) some large eggs were observed in the ovaries of females that were dissected. By the middle of May there were a few more and some eggs with brown coats far down in the oviduct were apparently ready to be laid. But at both of these times many ovaries were without large eggs. Throughout June and July eggs were readily collected in the field. Apparently eggs were laid during a period of more than two months, for eggs and larvae of various sizes were present in logs until the middle of August, when pupae appeared. Adults were present at all seasons, but eggs, larvae, and pupae were found only during the warmer months, when temperatures in logs in the forest averaged about 30° C. and air temperatures during the day averaged about 27° C.

Some seasonal variations in the parasites and commensals associated with Passalus in logs were also observed. These will be discussed in detail under the section on parasites. Subelytral and external mites were generally most abundant during cooler months and fewest in summer. Oribatids were found only during July and August. Gregarines, coelomic and enteric nematodes were erratic. The Dexiid fly, *Zelia vertebrata* Say, infested only large larvae and sometimes pupae, and was therefore present during late summer.

FOODS

METHODS

The larvae and adults of *Passalus cornutus* Fabricius used in the writers' experiments were collected from oak logs in various parts of the Duke Forest from June to September, 1935. In a few cases colonies were found in rotting pine, dogwood, and southern shagbark hickory, but never in seasoned woods. Adult beetles tunneled through the entire log but most eggs and larvae were found in the lower parts. The adults required little care in transportation but it was necessary to keep larvae cool and moist.

Several large colonies were kept in the laboratory for observation in aquarium jars or large finger bowls and provided with rotting oak wood in pieces large enough for burrows. Adults from different colonies were kept together but larvae to be kept safely with adults had to be with those from their own colony. Adults and larvae for stock purposes were cared for separately. In any case the wood was changed frequently; chiefly in order to maintain humidity as near optimum as possible.

Under laboratory conditions an adult Passalus weighing approximately 1.5 gms. eats an average of 0.5 gm. of oak wood, or one-third its body weight per day. Presumably this amount would be slightly greater under natural conditions. In the writers' work the following types of food were used: oak-wood agar, sweet potato agar, fungus cultures, midgut contents, seasoned wood, rotting oak-wood sawdust, rotting oak wood prepared by the adults, rotting oak wood sterilized, rotten prepared oak wood sterilized, rotting sterilized oak wood later prepared by adults, and seasoned wood inoculated with various fungi.

Larvae fed on agar, fungus cultures, and midgut contents were kept in petri dishes. These were changed every two or three days. Small larvae fed on various woods were kept in 250 cc. Erlenmeyer flasks. Cork stoppers fitted with glass tubing permitted ventilation without excessive evaporation. Large larvae were kept in finger bowls. A few drops of water were added every two or three days in all cases. Larvae were carefully removed daily from the flasks with tweezers and brushed with a camel's hair brush to remove all particles of dirt. Calipers were used for measuring and an analytical balance for weighing. The larvae were returned to their bottles immediately after being weighed.

All larvae were kept in a room where the humidity, as measured by a psychrometer, varied after the first week between 63% and 83%, and the temperature between 26° and 30° C., except for a week at the end of the experiments when the temperature was as low as 22° C. for two days. Although neither humidity nor temperature was constant, the range was less than that recorded by the Weather Bureau Station in Durham.

It was not possible to keep larvae in flasks as controls because the type of food necessary was not known. The only controls possible were larvae kept in large finger bowls with adults. Portions of the materials from burrows found in the forest were placed with these. Adults fed seasoned wood were kept in bell jars or finger bowls and those in sterilized wood were put directly in 500 cc. flasks in which the wood was sterilized. In these cases also a few drops of distilled water were added every two or three days.

EXPERIMENTS

In the first experiment six larvae ranging in size from 0.038 gm. and 12 mm. to 0.470 gm. and 28 mm. were each placed in 250 cc. Erlenmeyer flasks with only a few drops of water. The information as to how long these larvae would exist without food was desired to determine whether larvae in later experiments were feeding or not. The larvae were weighed and measured every day. One of the six lived two days, three lived three days, one four days, and one five days. Only half of these decreased in length every day

until death while the other three increased the second day and then decreased until death. Weights taken the last day showed an average decrease of 24%.

Sixteen larvae were put on oak-wood agar which was made by adding 25 grams of agar to a liter of liquid strained from boiling oak wood and water. This was done as one means of determining whether food essentials could be obtained from wood alone after destruction of fungi and bacteria, and it was also thought that if the extract did contain enough food it would be in a condition easily accessible. Six of the larvae were hatched on agar. They ranged from 0.02057 gm. and 11.5 mm. to 0.0300 gm. and 12 mm. when put on this medium; while ten others used ranged from 0.1160 gm. and 20 mm. to 1.3748 gm. and 42 mm. These larvae were weighed and measured every day. No newly hatched larva lived more than seven days; four lived three days, and one seven days. They showed an average increase of 19.9% in weight at the last observation. One decreased in length 13.0% before dying; two remained the same; while the three others showed an average increase in length of 7.1%. Of the larger larvae five showed an average increase of 9.91% in weight and a decrease of 0.3% in length. Five showed an average decrease of 15.7% in weight and 11.6% in length.

Attempts were made to feed seven larvae which ranged from 0.0500 gm. and 14 mm. to 0.1500 gm. and 17 mm. pure fungi on agar plates. Three of these were put on *Schizophyllum communa* and four on *Armillaria mellea*. These were weighed and measured only once a week to avoid contamination. Two larvae lived seven days; two, sixteen; two, twenty; and one, twenty-one days. The average increase in weight of all, except the two which lived only one week, was 23.8%; in length, 14.3%.

Twelve newly hatched larvae were fed material taken from the anterior midguts of adults, and weighed and measured daily. It was thought that this food would be the most suitable for young larvae since it would be well broken up and partially digested. The material was changed daily to avoid putrefaction. Larvae ranged from 0.0148 gm. and 10 mm. to 0.0254 gm. and 11 mm. All gained in weight and length remarkably at first but lived only a short while; two lived one day; four, two days; four, three days; one, four days; and one, five days. Two died the day after the experiment began so that no second observation was taken. The average increase in weight for the ten was 56.4%, in length 21.2%.

To test the belief that larvae are not able to exist and grow on sound seasoned wood forty-eight larvae were fed on this food and nothing else. They were weighed and measured every day for two weeks; then every other day. Twenty-four larvae decreased in weight and length before dying with an average decrease of 25.1% in weight and 17.1% in length; thirteen increased in weight and length before dying with an average increase of 33.8% in weight and 13.7% in length; four died the day after the experiment be-

gan; three increased in weight and decreased in length; three decreased in weight but showed no change in length; and one increased in weight and showed no change in length.

Nine large larvae were placed on rotten oak wood which had not been converted into sawdust to see if they would survive and grow. They were measured every three days. The larvae ranged from 0.3860 gm. and 27 mm. to 1.7010 gm. and 42.5 mm., and averaged 1.0458 gm. and 36.7 mm. Five of these became adults, one in thirty-two days, the others between sixty-three and seventy days. The others pupated but died soon after. Another larva died after being kept eighty-one days. One was parasitized by a fly larva and consequently killed.

Forty-three larvae ranging from 0.0209 gm. and 10.5 mm. to 0.4561 gm. and 26 mm. were fed rotten oak wood which had been converted into sawdust. This was done to determine if larvae required small particles of wood, such as that prepared by the adults and because small larvae did not seem able to chew whole rotten oak wood. With twenty-one of these newly hatched larvae wood was used in which no adults had been present. Twenty-four larvae lived two weeks or less, four between two and four weeks, ten between four and eight weeks, three between eight and fourteen weeks, and two between fourteen and seventeen weeks. Four pupated and one became an adult.

Forty-five larvae, including thirty-one newly hatched, and ranging from 0.0147 gm. and 10 mm. to 0.4524 gm. and 26.5 mm. were fed oak wood prepared by the adults, in an attempt to rear larvae from the egg to adult. The newly hatched larvae were measured daily at the beginning of the experiment, but later observed daily and measured every two or three days. Of the forty-five larvae, all increased in weight, one decreased 4.5% in length; twenty-five lived two weeks or less, four lived between two and four weeks, two between four and five weeks, two between eight and ten weeks, eight between ten and fourteen weeks, and one lived seventeen weeks and three days. Six of them became adults and two became pupae and died before becoming mature. Four of the larvae started were injured or eaten by other larvae and are not reported.

Two larvae, one 0.0267 gm. and 11 mm., the other 0.0227 gm. and 10 mm., were kept on rotten oak wood, which had been converted into sawdust and then sterilized. If these larvae had survived it would have eliminated the necessity of the preparation of wood by the adults, of the presence of fungi at the time of feeding, or the presence of living bacteria. The larvae were weighed and measured daily. One larva lived three days, the other seven. Since only two larvae were used in the experiment no definite conclusions can be drawn.

Thirteen larvae, ranging in size from 0.0183 gm. and 9 mm. to 0.0296 gm. and 11 mm. were kept on rotting oak wood prepared by the adults and then

sterilized. This was to determine if fungi or bacteria in the wood were necessary in the food. The larvae were measured and weighed every other day. All but one larva increased in weight and length. Three lived a week or less, five between one and two weeks, and four between two and three weeks (Table 1).

TABLE 1. Behavior of larvae fed on oak wood prepared by adult beetles and sterilized.

Beginning of expt.		End of expt.			Per Cent Increase	
Weight grams	Length mm.	Weight grams	Length mm.	Days of Life	Weight	Length
0.0183	9	0.0352	12	7	92.34	33.33
0.0296	11	0.0366	13	8	23.64	18.18
0.0288	11	0.0325	12	2	12.84	9.09
0.0272	11	0.0350	11	10	28.67	0
0.0266	11.5	0.0700	17	33	163.15	47.82
0.0231	11	0.0440	14	16	90.47	27.27
0.0236	12	0.0465	14	20	97.03	16.66
0.0236	11.5	0.0355	13	14	50.42	13.04
0.0200	10	0.0415	14	19	107.50	40.00
0.0238	11	0.0317	12	13	33.19	9.09
0.0253	11	0.0441	12.5	17	74.30	13.04
0.0252	11	0.0350	11.5	13	38.88	4.54
0.0214	11	0.0214	11	6	0	0

Four larvae were put on rotten, sterilized oak wood later prepared by adults, and weighed and measured every day. If larvae on rotten unprepared sterilized oak wood had died and these had lived, it would have shown that the adults in preparing the wood had changed it in such a way that it then had something necessary for life and growth. One larva lived six days, two seven days, and one ten days. All increased in weight and length before dying (Table 2).

TABLE 2. Behavior of larvae on oak wood prepared by adults.

Beginning of expt.		End of expt.		Days of life	Per Cent Increase	
Weight	Length	Weight	Length		Weight	Length
0.0274	12	0.0365	13.5	7	33.21	12.50
0.0278	12	0.0302	12.5	7	8.63	4.16
0.0295	12.5	0.0379	13	10	28.47	4.00
0.0275	11	0.0379	12.5	6	37.81	13.54

Five sets of experiments were tried in which fungi were allowed to act on sterilized, seasoned, sound oak wood for a definite period of time. The wood was then sterilized and inoculated with the larvae to see if they could complete the digestion of the wood which had been started by the fungus. Sterile sweet potato agar was added to the wood so that the fungi would grow more quickly. In the first case the fungi used were allowed to grow for seven

days, and three larvae were then introduced. These were weighed and meas-
ured only once a week in order to avoid contamination. The woods and fungi

TABLE 3. Behavior of larvae fed on oak wood on which fungi (Schizophyllum) were growing.

Wood	Beginning of expt.		Days of life	End of expt.		Per cent increase or decrease	
	Weight	Length		Weight	Length	Weight	Length
Post oak........ .	0.1800	20	43	0.2302	22	27.88	10.00
Black oak	0.1770	22	48	0.2540	24	43.50	9.09
Southern red oak.	0.3000	25	18	0.2623	23	—12.56	- -8.00

used and the record of larvae are given in Table 3. In another experiment the
fungi used were allowed to grow for sixteen days and five larvae were then
introduced. Table 4 shows the results. In a third experiment the fungi were

TABLE 4. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Beginning of expt.		Days of life	End of expt.		Per cent increase or decrease	
		Weight	Length		Weight	Length	Weight	Length
Black oak.	Polyporus...	0.4461	28	69	0.5860	30	31.36	7.14
Southern red oak .	Schizophyllum	0.4021	28.5	15	0.2500	20	-37.82	—29.82
Post oak..	Polyporus....	0.5800	32	69	0.5281	28	— 8.94	- -12.50
Post oak..	Schizophyllum	0.7328	35	69	0.8025	34	9.51	- - 2.85
Black oak.	Schizophyllum.	0.5784	31	40	0.5586	30	-- 3.42	—- 3.22

allowed to grow for twenty-two days. Two larvae were introduced (Table 5).

TABLE 5. Behavior of larvae fed on oak wood and fungus (Armillaria).

Wood	Beginning of expt.		Days of life
	Weight	Length	
Black oak...............	0.9302	36	Pupated in 18 days, died 74 days
Post oak................	1.2573	42	Pupated in 13 days, died 79 days

In a fourth experiment fungi were allowed to grow for twenty-three days
and four larvae were then introduced (Table 6). In a fifth experiment the

TABLE 6. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Weight	Length	Length of life
Black oak.... ...	Polyporus.......	1.0140	36	Pupated, 21 days. Died 29 days
Southern red oak...	Schizophyllum....	1.0181	36	26 days
Post oak..........	Polyporus........	0.9750	37	Pupated, 13. Adult 27
Post oak........ .	Schizophyllum....	1.0138	36	68 days

fungi were allowed to grow for thirty days. Three larvae were used (Table 7). Fourteen of all the larvae fed on wood and fungus died before pupating;

TABLE 7. Behavior of larvae fed on oak wood and fungus.

Wood	Fungus	Weight	Length	Days of life
Black oak.........	Schizopyllum.....	0.9791	36	51
Post oak..........	Polyporus........	0.6158	28	7
Black oak.........	Polyporus........	1.0950	38	Pupated 17, died 29 days

the remaining five pupated or became adults and then died.

To be sure that adults could not survive on seasoned woods, 48 were kept on seasoned woods which had not been broken up at all. The following woods were used: red cedar sapwood, red cedar heartwood, black gum, red gum, white ash, loblolly pine, shortleaf pine, southern shagbark hickory, mockernut hickory, mulberry, white oak, post oak, black oak, southern red oak, dogwood, and sourwood. Ten of the beetles lived a week or less, thirteen lived between one and two weeks, ten lived between two and three weeks, six lived between three and four weeks, one lived between four and five weeks, one between six and seven weeks, and one sixteen weeks. Later eight adults were put on seasoned southern red oak which was cut up and partly converted into sawdust to eliminate the possibility that the adults in the preceding experiment died because of inability to chew the seasoned wood. Two died after eleven days, one died in seventeen days, and the other five died in thirty-eight days.

Nine adults were kept on sterilized rotten oak wood. One died after twenty-nine days, one after fifty-seven days, while the seven others died after one hundred-sixty-eight days. Two adult beetles were kept in flasks with all conditions the same except that the food in this case was plain rotting oak wood. Both lived and were active throughout the experiment (168 days). When a beetle was placed in sterilized wood it may have introduced bacteria, but it probably did not introduce fungi. No fungi could be obtained from beetle gut-contents (adults) plated on agar, nor did visible mycelia grow in the inoculated wood. In other experiments inoculation of sterilized wood with fungi produced visible mycelia within a very short time.

Four colonies were kept in wood for observation. In the first, two adults were kept with two larvae and nine eggs. The two original larvae lived for forty-seven days, but both were finally destroyed, evidently by the adults. Three of the eggs hatched but the larvae from them were also killed. In the second colony eight larvae were kept with two adults. All of these also were destroyed either by the adults or by other larvae. At different times adults and large larvae were seen to kill small larvae from the same colony. In the third colony four larvae were kept but all were parasitized and consequently died. In the fourth colony also, in which eight larvae were kept with adults,

the larvae were all parasitized. However, in another large colony which was kept in a large aquarium jar with no particular attention, larvae hatched and developed to adults. Consequently it seems safe to assume that larvae would have lived under the same conditions as the experimental larvae and thus have served as controls if they had been given proper food.

DISCUSSION OF FOODS AND NUTRITION

Oak wood agar made up as described (p. 461) was not an adequate diet for Passalus larvae. Either it contained insufficient wood or it did not provide enough roughage, for later experiments showed that the same sort of wood was suitable for other larvae. Pure fungus did not contain all food essentials, as results on seven larvae fed it indicate. It took many more larvae to get favorable results in other experiments so that the small number here may have vitiated the results. However, other experiments point to the conclusion that wood is absolutely necessary. It is a question why no larva survived more than five days on midgut contents from adult beetles since that food was well broken up and partially digested. The larvae ate voraciously and increased remarkably in weight and length before dying in this experiment. Perhaps the food was too rich. Seasoned wood was not very suitable for food. One larva did live one hundred-eleven days on seasoned black gum and increased 124.77% in weight and 46.42% in length before dying, but it must have been exceptionally hardy. All others died much sooner.

All food essentials necessary for the development of Passalus larvae are present in rotting oak wood. Newly hatched larvae did not grow and pupate unless the wood was prepared by the adults. Larvae as small as 0.0300 gm. require wood that has been converted into sawdust. Even then it is difficult to rear them. This indicates that converting wood into sawdust in the laboratory does not render the wood as available as that prepared and left in mines as frass by adults. After reaching a weight of approximately 0.3800 gm., hardy larvae may metamorphose and become adults on rotten oak wood which has not been converted into sawdust. Such larvae have jaws strong enough to break up the wood, independently of the adult.

Experiments in which larvae were fed rotting oak wood prepared by the adults and then sterilized appear to indicate that the presence of fungi or bacteria in the wood at the time of feeding is necessary. However, larvae which were fed seasoned wood on which fungi had acted for thirty days and which was then sterilized, did metamorphose. In this case the presence of fungi or bacteria was not necessary. The larvae were of course larger when the experiment began. It seems logical to suppose that if a greater number of larvae had been fed rotting oak wood prepared by the adults and then sterilized, some would have metamorphosed. Adults have been kept for twenty-four weeks on sterilized rotten oak wood. They are as active as the controls,

thus substantiating the belief that the food essentials are found in rotten oak wood alone. Living fungi or bacteria do not appear to be necessary as ingredients of the food of adult Passali.

All adults which were raised in the laboratory were smaller in size than those found in the forest. It should be mentioned also that the rate of growth of larvae in the laboratory was noticeably less than that of those observed in the field. Unfavorable humidity conditions may have been responsible for such differences.

It would be desirable to rear more newly-hatched larvae on seasoned wood on which fungus has acted for certain periods of time before being sterilized, as in the experiments described. This would prove conclusively: (1) that the food essentials for larvae are in either rotted oak wood with the living fungi and bacteria or in rotted oak wood alone, and (2) how long fungi must act on the wood before it can be used as food.

There has been much discussion concerning the food requirements of insects which live in wood. Uvarov (1928) after an extensive review says:

It is known that the nutrition of the vast majority (perhaps of all) wood-feeding insects is intimately connected with their symbiotic micro-organisms, but the physiological side of their nutrition remains entirely unknown. Indeed all that is known is that the insects apparently feeding on wood, are not using wood directly as food. There is, however, no evidence at all as to what substances they do, in fact, feed on; these may be particles of wood partially digested by micro-organisms, or their secretions, or even the micro-organisms themselves. In other words, wood-eating insects must be classified as insects of absolutely unknown feeding habits.

There is no question that fungi produce a variety of enzymes which are capable of digesting lignin, cellulose, and other rather indigestible organic substances (Zeller, 1916). They are also known to contain Vitamin B (Gorcia, Peterson, and Steenbock, 1936), which is essential for the nutrition of many insects. Fungi are often found within insects and some types may have elaborate mechanisms for passing from one host to another (Schrader, 1923; Schwartz, 1932). Payne (1931) has shown conclusively that a particular fungus, *Armillaria mellea* Vahl., is necessary in the food of certain beetle larvae which live in oak bark. The beetles in question are usually annuals, but when fed on sterilized oak bark the larvae remained alive for as much as ten years without pupating. However, when a little unsterilized wood or fungus was added to the diet, the larvae pupated and the life cycle was completed in a short time.

In termites Hendee (1933, 1934) found no specific relation between particular species of fungi and nutritional requirements, although she isolated fifteen species of fungi from termites and showed that the insects are the primary agents in inoculating wood with fungus spores. Cleveland (1934) has accumulated considerable evidence to show that flagellate protozoans in

termites and blattids digest cellulose and convert it into soluble products like dextrose which are assimilated by the insect hosts.   Mansour and Mansour-Bek (1934) do not altogether agree with Cleveland's findings.   They studied the larvae of two cerambycid beetles and found that one was able to digest cellulose and that the other depended on sugars and starches present in wood; neither contained micro-organisms.   These men believe that insects which contain micro-organisms utilize them directly as food and do not assimilate the wood or other food which the organisms digest for their own needs.   In certain lamellicorn larvae bacteria appear to be the chief agents in breaking up cellulose in the intestine (Wiedemann, 1930).

No protozoans have been observed to be regularly present in the alimentary tract of *Passalus cornutus*.   There are at times gregarines in the midgut, but these probably play no important rôle in nutrition.   The larva of this beetle apparently belongs to the class of insects which live on rotten wood which contains fungi.   Very young larvae apparently also require something that the adult beetles add to rotten wood in chewing it and passing it through the gut.   Larger larvae flourish on rotten wood that has not even been finely divided and which has been sterilized.   Living fungi or bacteria are not essential in the food of adult Passali.

PARASITES AND COMMENSALS

METHODS

Passalus cornutus was collected from several localities in North Carolina at various seasons to examine its parasites and commensals, after which a more thorough and systematic survey was undertaken.   A particular area, entered from Gate 10 in the Duke Forest, was visited each month for an entire year.   At least ten beetles were collected on each field trip, five from logs on a hillside and five from logs at the base of the same hill near a small stream.   These were placed at once in separate rubber-stoppered bottles and carried to the laboratory.   No significant differences in parasites and commensals was observed between those from the higher, dryer regions and those from the lower, moister valley.

Collecting bottles were kept in a cold room at 4° C.   They were removed singly for examination within two days.   No beetles died before being studied. Each was carefully searched for external parasites; the cork and inside of the bottle were carefully examined with a binocular microscope.   Nothing but mites was found on the outside of the beetles.   Wings and legs were then removed, placed in a petri dish with the body of the beetle and all parts were again examined under a binocular microscope.   Mites were removed, counted, and preserved.   The body was then placed on a glass plate and dissected under a binocular microscope.   Clean water was added from a dropper at intervals while the dissection was in progress.   This kept the internal organs

from drying up before the small animals in them could be counted. The following annotated list describes the animals found and gives relevant information concerning them.

Phylum Protozoa
Class Sporozoea
Subclass Telosporidia
Order Gregarinida
Suborder Eugregarina
Legion Cephalina

Gregarina passali-cornuti Leidy

This gregarine was always found in the midgut, where it was attached to the wall or at times free in the lumen. During the year when routine monthly examinations were made no particular seasonal periodicity was observed. In June three lots of ten each from three different localities were
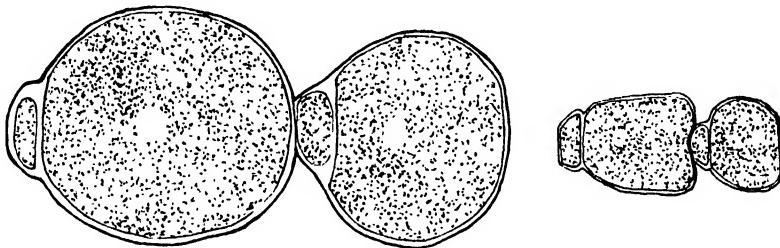
FIG. 2. *Gregarina passali-cornuti* Leidy: two pairs of individuals. The line indicates one millimeter.

examined. Among these six individuals from one lot contained gregarines, and none was found in the other two lots. Among the ten examined each month from the selected locality in the Duke Forest the following figures give the number of beetles infested and the average number of gregarines per individual: January, 1—1.8; February, 1—0.3; March, 1—2.0; April, 0.0; May, 0.0; June, 4—6.1; July, 0.0; August, 0.0; September, 0.0; October, 0.0; November, 2—9.6; December, 2—4.2; average 0.9—1.7.

Phylum Nematoda
Class Phasmidea
Order Rhabditida
Family Rhabditidae
Subfamily Thelastomatinae

Histrignathus rigidus Leidy

This parasite lives in the anterior end of the pyloric section of the enteron. Christie (1934) has described two forms of this nematode, which differ in the number and arrangement of dermal spines. These have been called *H. rigidus*

Leidy and *H. histrix* (Cobb). As they occur together in *Passalus cornutus*
they are perhaps merely forms of one species and the writer therefore uses
the earlier name, though both occur in the beetles in the Duke Forest. Christie
says "there is the possibility that we are dealing, not with 2 species, but with
a single, polymorphic species in which occur 2 types of females and 1 type
of male."

This nematode was found during every month in the year, with the largest
numbers in April, July, August, and November and the smallest numbers in
February, June, and September; so there appears to be no significant variation
correlated with different seasons. The number of beetles infested and the
average number of parasites per host in the ten beetles examined each month
were as follows: January, 6—3.5; February, 3—1.5; March, 8—3.9; April,
8—8.7; May, 8—6.1; June, 2—2.6; July, 7—5.6; August, 8—5.9; September,
5—1.0; October, 5—3.7; November, 7—8.8; December, 2—1.2; average,
5.4—4.4.
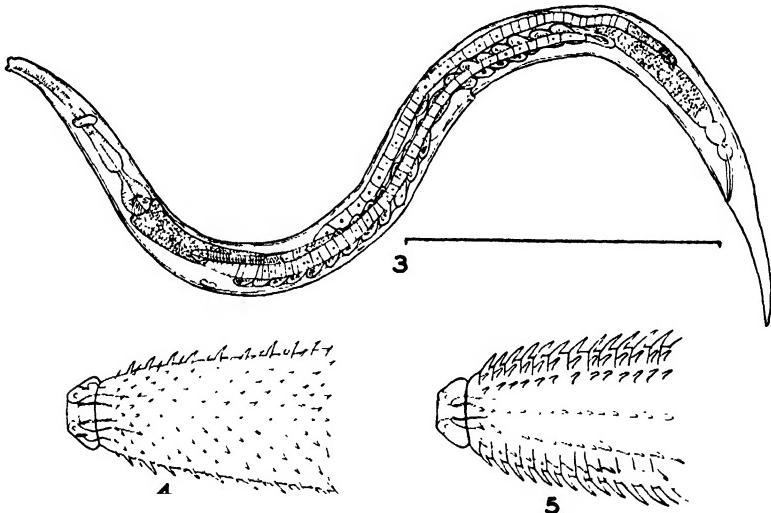
FIGS. 3-5. *Histrignathus rigidus* Leidy; after Christie (1934): 3, female;
4, anterior end of *H. histrix* form; 5, anterior end of *H. rigidus* form.

Chondronema passali (Leidy)

This nematode lives in the body-cavity of Passalus. Christie and Chit-
wood (1931) have made an extensive study of the parasite. They say:

The parasites enter the host as very young larvae. That the beetles are
being continually infected is indicated by the fact that very young parasites
are present regardless of the age of the beetles or the time of the year when
they are collected. It seems to us probable that the larval parasites are taken
per os while the beetles are feeding. The exceedingly heavy infestations en-
countered suggests the possibility that the mother nemas may be swallowed.
. . . Whenever beetles were killed and placed in cultures of moist, decayed

wood, all the body-cavity parasites died, which seems to render the possibility of the parasites being liberated through the death of the host unlikely. The oldest of the body-cavity parasites were on many occasions removed from the beetles and placed in moist decayed wood and various other types of cultures, but they always died. . . . We therefore concluded that . . . the adult nemas live free in moist, decayed wood or frass; and, after many hours of tedious searching of such material, we finally discovered the adult nema.

This species, as judged by our routine monthly examinations in the Duke Forest increases greatly in numbers in late summer. This is probably due to the fact that after September there are many beetles which have recently emerged from pupae and have not yet become infested or contain only a few worms. During the summer the degree of infestation steadily increases and reaches a maximum average just before the new brood of a year begins to
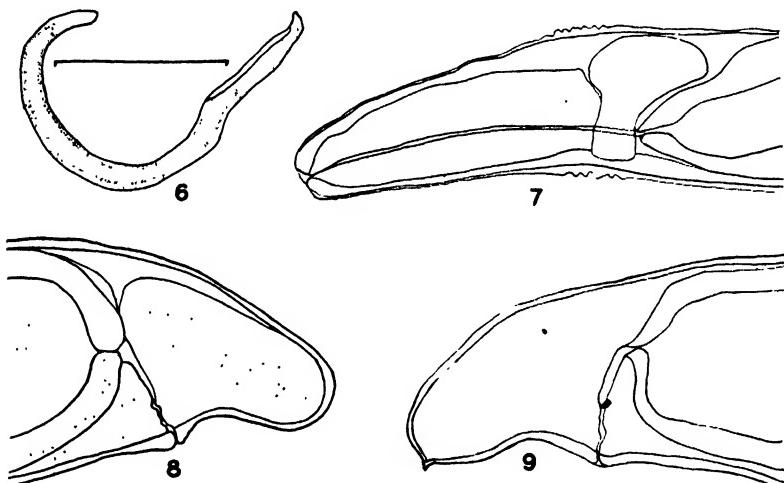
FIGS. 6-9. *Chondronema passali* (Leidy) : 6, side view of worm from body cavity ; 7, anterior end ; 8, posterior end without spine ; 9, posterior end with spine.

emerge, but an individual may continue to accumulate worms throughout its life. In one instance about 4,260 were counted in a single beetle (August). The number of beetles infested in each month and the average number of parasites per host were as follows: January, 10—57.7; February, 10—95.6; March, 10—68.1; April, 10—133.0; May, 9—79.5; June, 10—228.1; July, 10—324.0; August, 10—1,028.0; September, 10—3,274.7; October, 7—46.3; November, 9—140.5; December, 10—130.8; average, 9.6—467.2.

Phylum Arthropoda
Class Arachnida
Order Acarina

The seasonal occurrence of all species of mites found associated with *Passalus cornutus* is shown in Table 8. In studying these mites much

help was received from Dr. H. E. Ewing who examined our material and loaned specimens from the United States Museum for comparison. All new species in this paper were described by A. S. Pearse and G. W. Wharton and have been examined by Dr. Ewing.

Suborder Parasitina
Family Parasitidae
Subfamily Parasitinae

Megisthanus floridanus Banks

This large, flat mite was never abundant and at times none was collected from the ten Passali which were examined each month. It ran freely over the surface of its host, and was never found beneath the wings. This species is readily recognized by the strong teeth on the posterior borders of the hind femora.
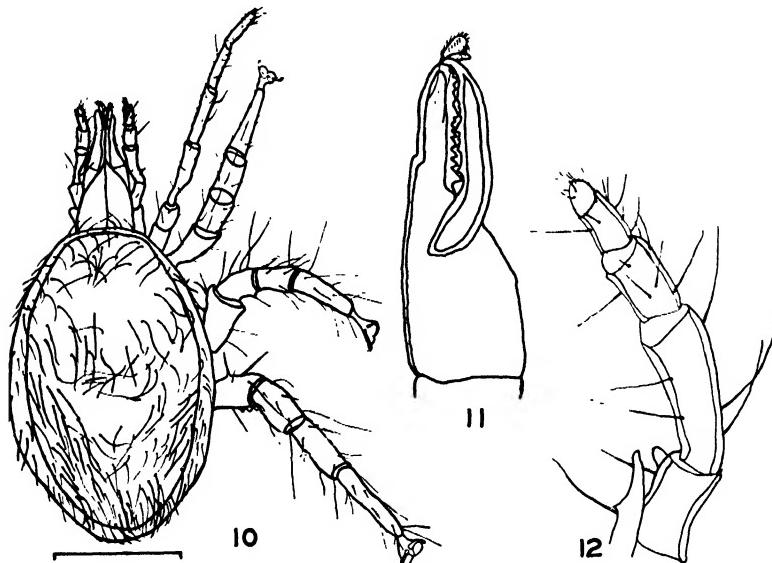
FIGS. 10-12. *Megisthanus floridanus* Banks: 10, dorsal view; 11, tip of chelicera; 12, pedipalp.

The body is oval in outline, the anterior sixth sharply constricted; both ends rounded; length 0.83 mm.; width, 0.52 mm., of the constricted anterior sixth, 0.23 mm. On the anterior margin are two delicate setae; behind these there are four rows of four small setae across the dorsum and a pair near the middle; along the lateral margins are eleven pairs of setae. The ventrum has three median plates; sternal, genital, and ventro-anal; these bear setae as follows: 6, 4, 10. The male genital aperture is in front of the sternal plate; the female aperture in front of the genital plate between the bases of the third legs.

Macrocheles tridentatus n. sp.

The chelicerae are chelate; the dactyl bears two blunt, rough, recurved teeth on its distal half and has a curved tip; the fixed finger has a stout tooth near its tip; a plumose hair stands at the base of the dactyl. The pedipalpi are 5-segmented; in order of length the segments rank: 5, 4, 2, 3, 1; all are somewhat setose and there is a group of small setae at the tip of segment five. The hypostome bears two setae; a median, tapering setose process; and two slender, pointed, lateral teeth. The legs are all shorter than the body; in order of length they rank: 4, 1, 3, 2; each is setose and the last three also bear a pair of spines and a caruncle at the tip.
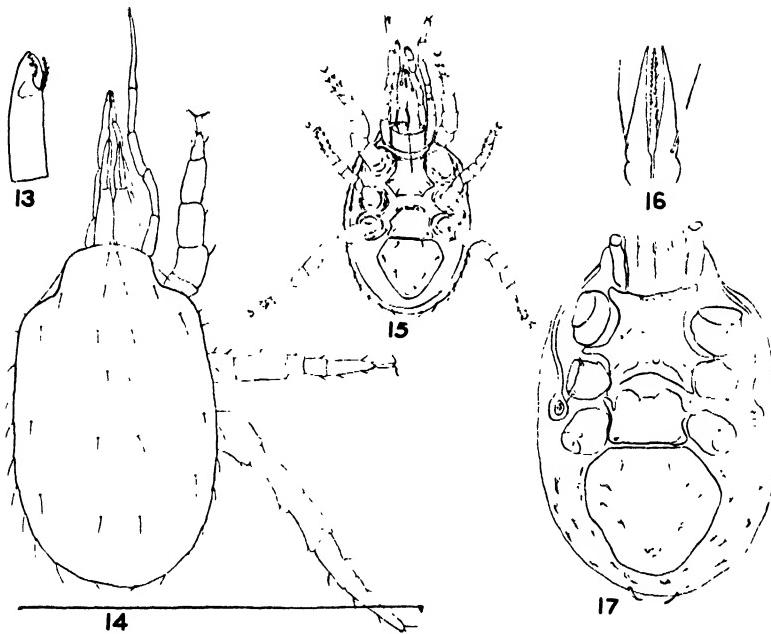
FIGS. 13-17. *Macrocheles tridentatus* n. sp.: 13, tip of chelicera; 14, dorsal view; 15, nymph; 16, mouth parts; 17, ventral view of female.

Types, male and female (U. S. Nat. Mus. No. 1172) : on *Passalus cornutus* Fabricius, Duke Forest, Durham, N. C.; June 7 and September 17, 1933; respectively; Collector, A. S. Pearse. The specimen is named for its trident hypostome.

The body is almost 1 mm. long, oval in outline and somewhat truncate at each end. The dorsum bears about fifty rather stout setae; there are ten to fourteen more setae along the posterior margin and two at the anterior end; the antero-lateral regions are without setae. The ventrum has three plates: sternal, gental, and ventro-anal, which bear setae as follows: 6, 4, 28. The male genital aperture is in front of the sternal plate; the female aperture is in front of the genital plate.

Sciodes trifidus n. sp.

The chelicerae are chelate; the dactyl bears two blunt teeth on its distal half and has a curved tip; the fixed finger has about thirteen small teeth near its recurved tip. There is a transverse row of setae at the base of the dactyl on the palm. The pedipalpi are 5-segmented; in order of length the segments are: 4, 3, 1, 2, 5; all are somewhat setose and there is a group of setae at the tip of Segment 5. The hypostome bears four ventral setae and ends in a trident (hence *S. trifidus*); from its dorsal surface a conical setose tooth projects anteriorly. The legs each bear two claws and a caruncle; they are well armed with stout setae; in order of length they rank: 1, 4, 2, 3.
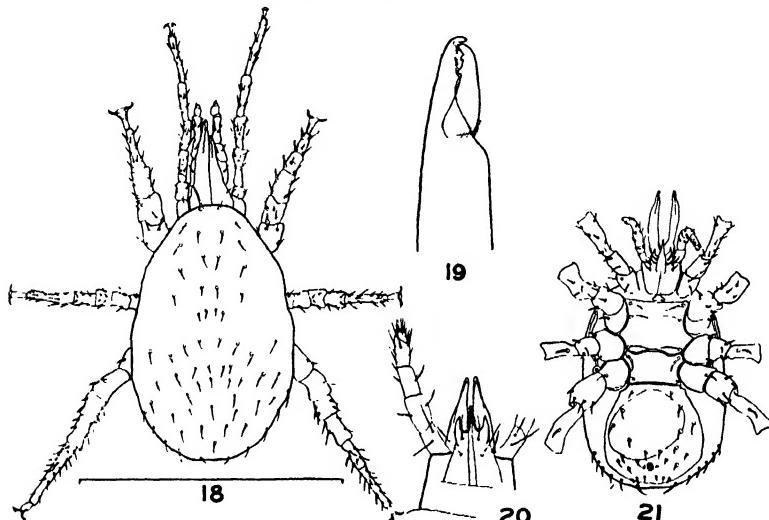
FIGS. 18-21. *Sciodes trifidus* n. sp.: 18, dorsal view; 19, tip of chelicera; 20, hypostome, tip of chelicera, and pedipalp; 21, ventral view of female.

Type (U. S. Nat. Mus. No. 1179): on *Passalus cornutus* Fabricius, Duke Forest, Durham, N. C., June 27, 1933; Collector, A. S. Pearse.

Mites belonging to this species usually rested in the spaces between the legs or between the body regions of Passalus. When disturbed they ran rapidly about over their hosts.

Caelenopsis latus Banks

This species is peculiar among those which occur on Passalus, in having clearly defined and separate ventral, lateral, and anal plates. It was somewhat more common in autumn than at other seasons. Its distribution and behavior on the body of its host were about the same as those of the last species.

Passalacarus n. gen.

Parasitinae. The first legs are without caruncles or claws, and thus agree with those in the genera Podocium, Rhodocarus, Caelenopsis, Euzercon, Macro-

cheles, Megisthanus, and the Antennophori. The dorsal shield is undivided, as in the last four genera mentioned. The ventrum shows lateral plates and thus agrees with Euzercon and Caelenopsis. Passalacarus is distinct from the short-legged Antennophori, for the representatives of the new genus have legs considerably longer than the width of the body. It most closely resembles Macrocheles, but differs from that genus in the following characters: the dorsum is setose at the margins and toward the posterior end, but bears few setae on the middle and anterior surfaces; the shape of the body is oval with the posterior end pointed in both sexes; the fused anal and ventral plates are thus elongated and tapering posteriorly; the chelicera has a flat, jointed appendage and a plumose seta at the base of its dactylus; the hypostomal plate bears a semicircular disc with radiating setae below, four stout spines, and a terminal conical process with two setae at its tip.

Type Species: *P. sylvestris* Pearse and Wharton.
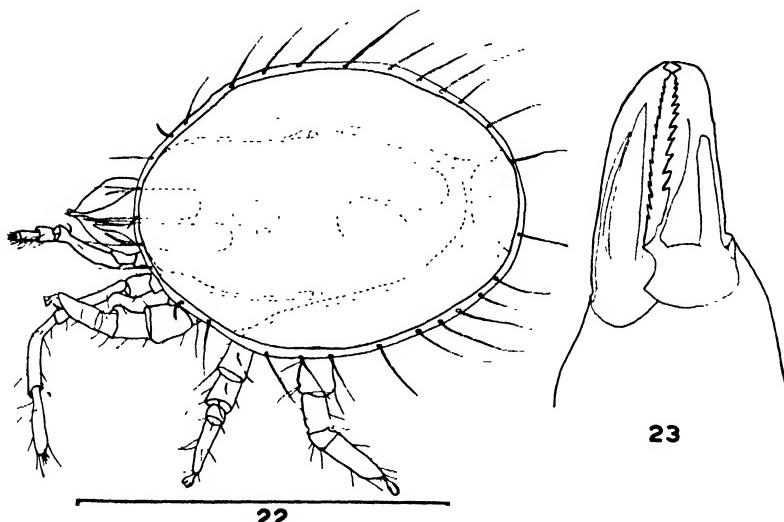
FIGS. 22-23. *Caelenopsis latus* Banks: 22, dorsal view; 23, tip of chelicera.

Passalacarus sylvestris n. sp.

The body is conical, tapering somewhat toward the posterior end; 0.90 mm. long, 0.54 mm. wide. The dorsum is flat, but slightly elevated; with 36 setae around the margin of the posterior three-fourths, four complete and two partial transverse rows in the posterior third, nine transverse groups of one to three along each margin, three pairs along the median line on the anterior half, one median seta on the anterior margin. The ventrum shows a large median plate and two slender marginal plates in the posterior two thirds. There are two (♀) or four (♂) transverse rows or setae on the posterior third and two pairs on the anterior half there are four or five pairs. The

male genital aperture is in front of the sternal plate; that of the female is between the bases of the third legs. The stigma is opposite the coxa of the fourth legs and the peritreme curves forward around the base of the first leg. The eggs within the female are ovate; 0.16 mm. long.
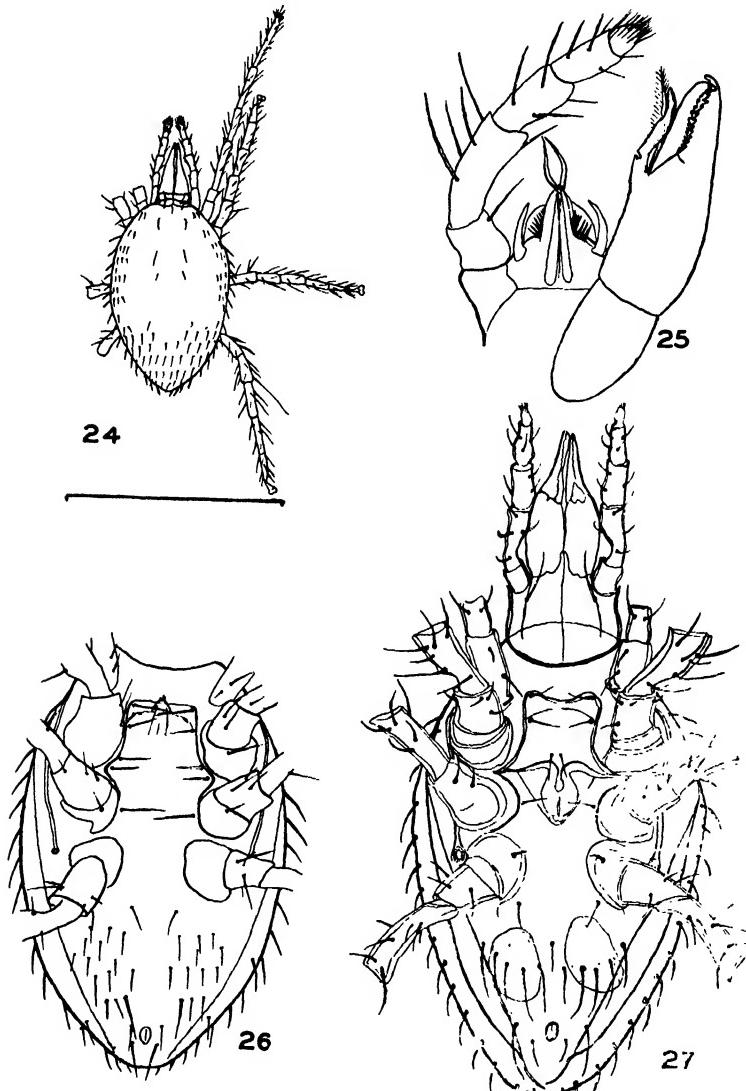
FIGS. 24-27. *Passalacarus sylvestris* n. sp.: 24, dorsal view; 25, pedipalp, hypostome, and chelicera; 26, ventral view of male; 27, ventral view of female.

The chelicera (Fig. 25) is 2-segmented; the movable dactyl is toothed on its inner margin and hooked at its tip; at its base the palm is produced into a flat, jointed appendage and bears a plumose seta; the dactyl is less than half

as long as the basal segment. The pedipalp is 5-segmented; the first segment is less than half as long as the second; the third is two-thirds as long as the second; the fourth, slightly shorter than the third; the fifth half as long as the fourth and setose; the pedipalp is also sparsely setose throughout the segments from base to tip bearing the following numbers of setae: 1, 5, 4, 5, 20. The hypostome is as described under the genus. The legs are setose; the first is longer than the body and bears no caruncles and two claws; the second and third are nearly equal and shorter than the fourth.

Types, male and female (U. S. Nat. Mus. No. 1175) Duke Forest, Durham, N. C., May 19, 1934 and August 19, 1933, respectively; on *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

In the Duke Forest this species occurred in maximum numbers in the autumn (Table 8). It was always found on the outside of Passalus.

Zercon passsalorum n. sp.

The body is elongated, oval in outline, tapered and rounded at the anterior and truncated at the posterior end; length, 0.31 mm.; width, 0.17 mm. There are four stout setae on the posterior border; ten setae along each lateral margin, and eleven on the dorsum near the margin. The dorsum is divided into approximately equal anterior and posterior halves by a transverse groove. There are five pairs of setae along the median line behind the groove and
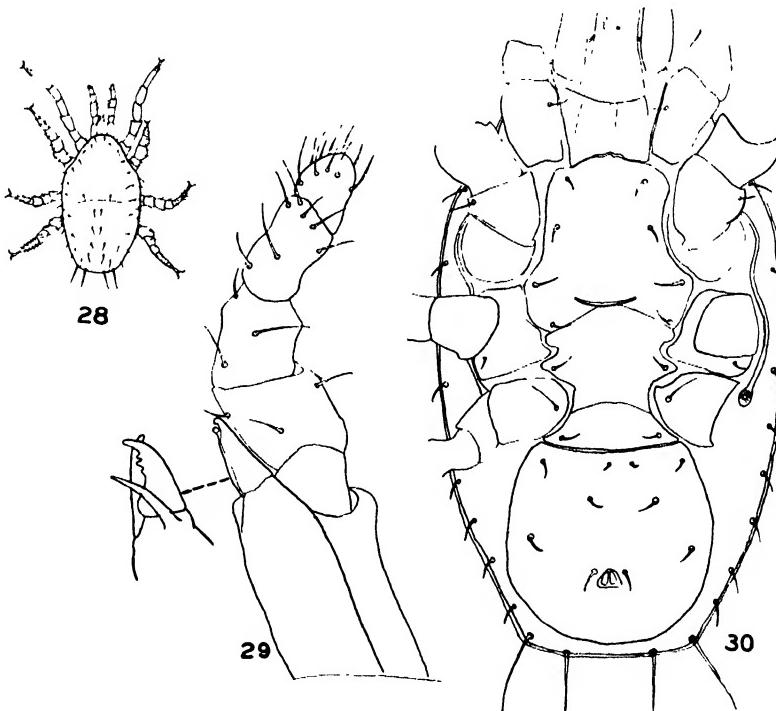
FIGS. 28-30. *Zercon passalorum* n. sp.: 28, dorsal view; 29, chelicera and pedipalp; 30, ventral view of male.

another just anterior to it. The ventrum of the male shows two median plates, a sterno-genital plate between the legs, and a ventro-anal plate behind. There are six pairs of setae along the lateral margins of the former and ten on the latter. The stigma is opposite the fourth coxa and the peritreme follows a sinuous course forward. The male genital aperture is a curved transverse slit in the middle of the sterno-genital plate. The female has a large ventro-anal plate which occupies most of the space behind the posterior pair of legs.

The chelicerae are chelate; the dactyl is about a fourth as long as the basal segment; it bears three teeth on its distal half. A conical curved process arises from the basal segment at the base of the dactyl. The pedipalp is 5-segmented; the second segment is longer than the first; the second, third and fourth grow progressively a little longer; the terminal segment is about half as long as the fourth, and setose. The legs each terminate in a caruncle and two claws; they bear short setae throughout, except the first pair which are setose only on the tarsus; from longest to shortest they may be arranged in the following order: 1, 4, 3, 2; the first leg is slightly shorter than the length of the body.

Types, male and female (U. S. Nat. Mus. No. 1173) : Duke Forest, Durham, N. C.; August 19, 1934; under wings of *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This species was common the year round under the wings of Passalus and the numbers increased greatly in the winter (Table 8).

Subfamily Uropodinae
Uroscius quercus n. sp.

The body is oval in outline; both ends rounded; tapering a little anteriorly; flat; length, 0.42 mm.; width, 0.27 mm. On the dorsum along the middle third of each side are three plumose setae which are slightly longer than the body; across the posterior margin are eight slightly shorter plumose setae. The anterior margin projects over the bases of the mouth parts and the first pair of

FIGS. 31-34. *Uroseius quercus* n. sp.: 31, ventral view; 32, dorsal view without appendages; 33, ventral view of mouth parts, 34, chelicera.

legs. The ventrum bears six short hairs at the anterior margin in two long-itudinal rows close to the bases of the coxae. The anus is on the posterior margin. The female aperture is a slightly curved transverse slit between the bases of the third legs. The male aperture is in front of the bases of the first legs between a pair of conical, anteriorly directed processes on the sternal plate. The stigma is opposite the anterior border of the base of the fourth leg; the peritreme is very short and straight.

The chelicera is chelate; on the inner margin of both the fixed finger and on the dactyl is a poorly defined tooth near the curved tip; the dactyl is about a third as long as the basal segment; a conical process arises near the base of the fixed finger and extends beyond the tip of the segment. The pedipalpi are 5-segmented; the segments increase progressively in length to the fifth, which is about as long as the first and setose; the second segment bears a single long seta. The hypostome is elongated and made up of two conical processes, each of which bears a horse-shoe shaped sculpture near its tip; distal to these marks are two stout acute lateral spines. The legs are short; the first pair are with-out caruncles or claws; according to length they rank in the following order: 4, 3, 2, 1; the fourth leg is slightly less than the width of the body; the legs are sparsely provided with plumose and naked setae.

The larva has long setae on its legs as well as its body; those on the body are limited to four along the posterior border.

FIGS. 35-36. *Uroobovella setosa* n. sp., nymph: 33, ventral view; 34, left peritreme.

Types, male and female (U. S. Nat. Mus. No. 1174): Duke Forest, Durham, N. C.; August 18, 1933 and May 19, 1934; on *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This little mite is usually found on the outside of Passalus, where it lurks in the crevices between the parts near the anterior end, but sometimes it creeps under the elytra. It is very slow in its movements. This fact and the very long setae on its body make it easy to recognize. It occurred in considerable numbers throughout the year on Passali in rotting logs in the Duke Forest.

Uroobovella setosa n. sp.

Only attached nymphs were collected. The adults are probably free-

another just anterior to it. The ventrum of the male shows two median plates, a sterno-genital plate between the legs, and a ventro-anal plate behind. There are six pairs of setae along the lateral margins of the former and ten on the latter. The stigma is opposite the fourth coxa and the peritreme follows a sinuous course forward. The male genital aperture is a curved transverse slit in the middle of the sterno-genital plate. The female has a large ventro-anal plate which occupies most of the space behind the posterior pair of legs.

The chelicerae are chelate; the dactyl is about a fourth as long as the basal segment; it bears three teeth on its distal half. A conical curved process arises from the basal segment at the base of the dactyl. The pedipalp is 5-segmented; the second segment is longer than the first; the second, third and fourth grow progressively a little longer; the terminal segment is about half as long as the fourth, and setose. The legs each terminate in a caruncle and two claws; they bear short setae throughout, except the first pair which are setose only on the tarsus; from longest to shortest they may be arranged in the following order: 1, 4, 3, 2; the first leg is slightly shorter than the length of the body.

Types, male and female (U. S. Nat. Mus. No. 1173): Duke Forest, Durham, N. C.; August 19, 1934; under wings of *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This species was common the year round under the wings of Passalus and the numbers increased greatly in the winter (Table 8).

<center>Subfamily Uropodinae
Uroscius quercus n. sp.</center>

The body is oval in outline; both ends rounded; tapering a little anteriorly; flat; length, 0.42 mm.; width, 0.27 mm. On the dorsum along the middle third of each side are three plumose setae which are slightly longer than the body; across the posterior margin are eight slightly shorter plumose setae. The anterior margin projects over the bases of the mouth parts and the first pair of

FIGS. 31-34. *Uroseius quercus* n. sp.: 31, ventral view; 32, dorsal view without appendages; 33, ventral view of mouth parts, 34, chelicera.

legs. The ventrum bears six short hairs at the anterior margin in two long-itudinal rows close to the bases of the coxae. The anus is on the posterior margin. The female aperture is a slightly curved transverse slit between the bases of the third legs. The male aperture is in front of the bases of the first legs between a pair of conical, anteriorly directed processes on the sternal plate. The stigma is opposite the anterior border of the base of the fourth leg; the peritreme is very short and straight.

The chelicera is chelate; on the inner margin of both the fixed finger and on the dactyl is a poorly defined tooth near the curved tip; the dactyl is about a third as long as the basal segment; a conical process arises near the base of the fixed finger and extends beyond the tip of the segment. The pedipalpi are 5-segmented; the segments increase progressively in length to the fifth, which is about as long as the first and setose; the second segment bears a single long seta. The hypostome is elongated and made up of two conical processes, each of which bears a horse-shoe shaped sculpture near its tip; distal to these marks are two stout acute lateral spines. The legs are short; the first pair are with-out caruncles or claws; according to length they rank in the following order: 4, 3, 2, 1; the fourth leg is slightly less than the width of the body; the legs are sparsely provided with plumose and naked setae.

The larva has long setae on its legs as well as its body; those on the body are limited to four along the posterior border.

Types, male and female (U. S. Nat. Mus. No. 1174): Duke Forest, Durham, N. C.; August 18, 1933 and May 19, 1934; on *Passalus cornutus* Fabricius; A. S. Pearse, Collector.

This little mite is usually found on the outside of Passalus, where it lurks in the crevices between the parts near the anterior end, but sometimes it creeps under the elytra. It is very slow in its movements. This fact and the very long setae

FIGS. 35-36. *Uroobovella setosa* n. sp., nymph: 33, ventral view; 34, left peritreme.

on its body make it easy to recognize. It occurred in considerable numbers throughout the year on Passali in rotting logs in the Duke Forest.

Uroobovella setosa n. sp.

Only attached nymphs were collected. The adults are probably free-

living. The body is flat and oval in outline; length, 0.57 mm.; width, 0.44 mm. The dorsum is rough, pitted and finely tuberculate; without setae. The ventrum has a thickened rim around the margin; impressed foveae for the legs, and well defined anal and ventral plates; setae around the whole margin; and a camerostome which receives the first legs and mouth parts when retracted. The slender chelate chelicerae are about 5/8 as long as the body; the dactyl less than 1/12 as long as the basal segment when retracted within the body. The pedipalp is short; the segments fall in the following order according to length: 4, 1, 2, 3, 5; the tip is setose. The legs all bear a pair of claws and a caruncle at their tips; the tarsi are somewhat pedicellate, with a few short setae, the first pair more than the others. The legs are about equal in length. The stigma is slightly anterior to the third pair of legs. The peritreme is slender with a short, curved, posterio-median branch and a very sinuous anterior trunk extending forward beside the camerostome.

Type (U. S. Nat. Mus. No. 1177): Duke Forest, Durham, N. C.; August 14, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This nymphal mite with other species of uropodids was commonly found attached by anal filaments in the cavities on the ventral side of the head of Passalus. It was less common than the next species.

Uroobovella spinosa n. sp.

Only nymphs have been collected. The body is oval in outline slightly tapered anteriorly; length, 0.37 mm.; width, 0.23 mm. The foveae for the reception of the legs are deeply impressed into the ventrum and the marginal thickening is heavy. Along the margin are about twenty pairs of curved spinose setae. The anterior margin projects over and conceals the retracted mouth parts and first legs in the camerostome; it is truncate and bears two curved setae. The sternoventral plate is constricted between the

FIG. 37. *Uroobovella spinosa* n. sp. nymph: ventral view.

bases of the fourth legs, there are three pairs of small setae in front. The anal plate is almost round and bears three pairs of small setae. The stigma is lateral to the bases of the third legs. The peritreme is sinuous.

The chelicerae are slender, chelate, and when retracted are almost three-fifths of the length of the body; the dactyl is about one-sixteenth of the length of the basal segment. The pedipalp is slender and 5-segmented. The legs

are all shorter than the width of the body. Each bears a pair of spines and a caruncle at its tip; all are sparsely setose. The bases of the first legs are indented on their anterior margin.

Type (U. S. Nat. Mus. No. 1178): Duke Forest, Durham, N. C., July 19, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This species was not as common as the others in the same genus.

Uroobovella levis n. sp.

Only nymphs have been collected. Body flat and almost elliptical in outline, slightly tapered anteriorly; length, 0.28 mm.; width, 0.22 mm. The dorsum is smooth, but there is a pair of small setae at both the anterior ends and a few very minute setae along the margins. The ventrum has a wide thickened margin, and impressed foveae for the legs; the posterior border of the camerostomal opening is somewhat convex; the triangular ventral and
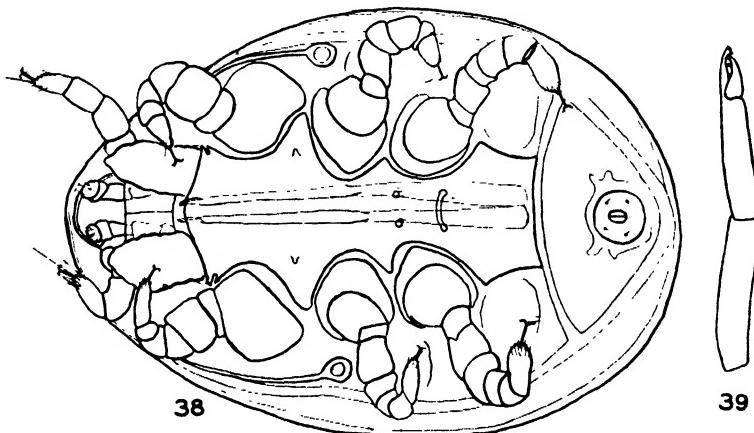
FIGS. 38-39. *Uroobovella levis* n. sp., nymph: ventral view; 39, chelicera.

nearly circular anal plates are clearly defined; a pair of short spines between the second and third legs. On the dorsum there are a pair of small setae near the posterior margin. The curved female genital aperture is between the bases of the fourth pair of legs. The stigma is opposite the anterior border of the third pair of legs; a slightly curved peritreme extends forward from it along the side of the camerostome. All legs are provided with short pedicellate, setose tarsi, a pair of claws, and a caruncle; they are about as long as half of the width of the body and nearly equal in length. The chelicerae are a little more than half as long as the body when retracted; chelate, with the dactyl almost 1/15 of the length of the basal segment. The pedipalpi are slightly clavate and long enough to reach nearly to the anterior end of the body when retracted; the first segment is twice as long as the second, third, and fourth, which are subequal; the fifth segment is setose and hemispherical.

Type (U. S. Nat. Mus. No. 1176); Duke Forest, Durham, N. C.; August 18, 1933; on *Passalus cornutus* Fabricius; Collector, A. S. Pearse.

This mite was commonly found attached in the hollows beneath the head of Passalus. It occurred at all seasons and was, in individuals, most numerous of any species in the genus Uroobovella.

Suborder Oribatina
Family Hoplodermatidae
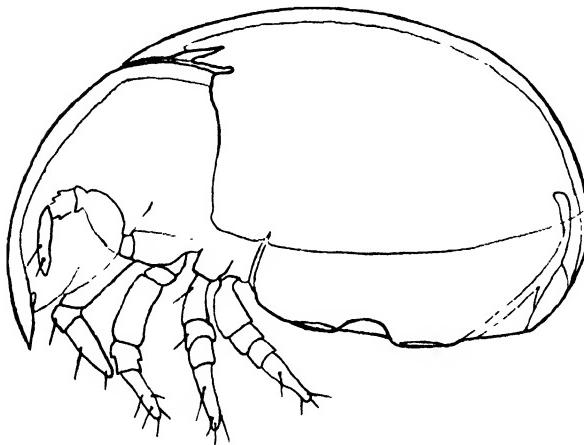
FIG. 40. Side view of hoplodermatid mite.

In June and July, 1933, a few of these peculiar mites were found on Passalus. They are readily recognized because of the cephalothorax being movably attached to the abdomen, so that the animal is able to roll up like an armadillo with the legs concealed. The specimens collected represented new genera and species. They were presented to Dr. H. E. Ewing for study.

Suborder Sarcoptina
Family Canestriniidae

Heterochelytus fusiformis Lombardini

This species was recently described (Lombardini, 1926) from passalids in Brazil. On *Passalus cornutus* in the Duke Forest it was found at all seasons beneath the elytra, and was therefore often associated with *Zercon passalorum*.

Family Tyroglyphidae
Hypopi

At all seasons nymphal hypopi were found on Passalus and beneath the elytra, maximum numbers occurring in the au-

FIG. 41. Ventral view of *Heterochelytus fusiformis* Lombardini.

tumn (Table 8). They could not be identified but two of the types are figured.
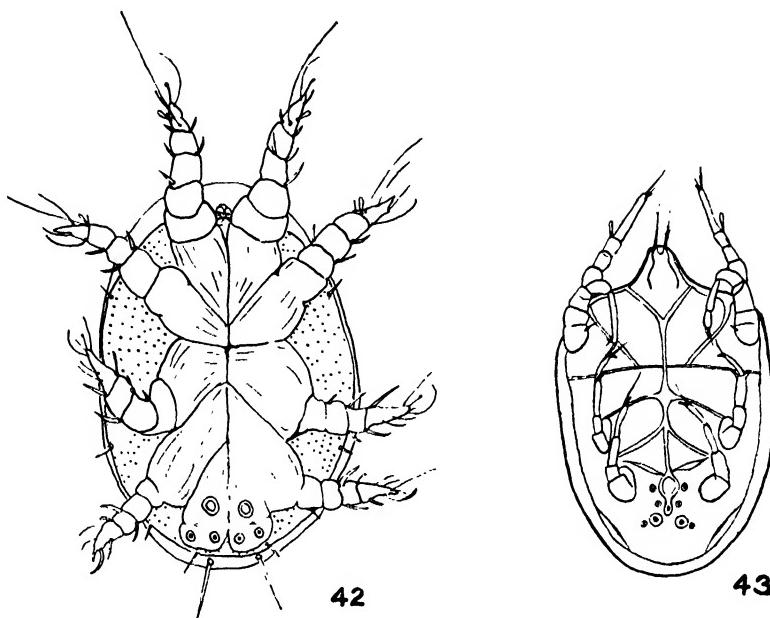
FIGS. 42-43. Ventral views of two hypopi.

Class Insectea
Superorder Dipterea
Order Dipterida
Suborder Brachycerina
Family Dexiidae
Zelia vertebrata Say

The larvae of this handsome fly were found in well grown larvae and pupae of Passalus in August and September 1933, and were very common in larvae in the autumn of 1935. Specimens were identified by Mr. David G. Hall, of the United States Bureau of Entomology.

DISCUSSION OF COMMENSALS AND PARASITES

Some of the animals associated with Passalus are probably parasites. Among these are perhaps Gregarina; the nematodes, Chondronema and Histrignathus; Heterochelytus, and the fly Zelia. Probably all the other animals are commensals; the mites: Megisthanus, Macrocheles, Caelenopsis, Passalacarus, Zercon, Uroseius, Uroobovella, hoplodermatids, hypopi.

Some of the animals which commonly live on or in Passalus show well marked seasonal distribution, others are erratic or evenly distributed throughout the year. The following list gives a general idea of conditions found by

TABLE 8. Mites on *Passalus cornutus*. Average number per month; June, 1933 to May, 1934. The first figure in each space indicates mites found on the exterior; the second, those found under the wings.

Month	January	February	March	April	May	June	July	August	September	October	November	December	Ave.
Number examined	10	10	10	10	10	10	10	10	10	10	10	10	
Magisthanus	0.5	0.7	0.2	0.2	0	...	...	...	0.3	0.3	0.1	0	0.26
floridanus	0	0	0	0	0	...	...	...	0	0	0	0	0
Macrocheles tridentatus;	0.2	4.5	1.6	2.3	0	...	...	...	2.0	2.7	2.0	0.9	1.80
Seidoes trifidus	0	0	0	0	0	...	...	...	0	0.1	0	0	+
Passalacarus	2.2	4.1	0.4	2.3	2.8	...	...	...	5.0	4.6	6.1	1.5	3.22
sylvestris	0	0	0	0	0	...	...	...	0	0	0	0	0
Caelenopsis	1.5	1.7	0.3	1.2	0.4	...	...	...	1.3	2.4	2.6	0.8	1.36
latus	0	0	0	0	0	...	...	...	0	0	0	0	0
Zercon	0	0	0	0	0.1	...	0	0	0	0	0	0	+
passalorum	22.5	58.7	100.3	8.6	6.0	...	10.3	7.8	12.1	5.5	11.7	81.4	29.54
Uroseius	2.1	6.1	6.3	2.3	3.4	..	5.2	9.9	4.5	1.4	4.2	6.5	4.72
quercus	0	0	0	0	0.3	...	0.1	0	0.4	0.2	0.4	0	0.13
Uroobovella*	5.0	35.9	46.2	27.7	2.4	15.7	96.1	9.7	23.5	18.2	62.1	16.6	29.93
3 species	0	0	0	0	0	0	0	0	0	0	0.1	0	+
Heterochelytus	0	0	0	0	0	...	0	0	0	0	0	0	0
fusiformis	7.7	6.2	6.0	2.8	7.7	...	5.6	2.2	6.8	0.9	6.1	8.6	5.51
Hypopi	2.1	0.4	0	0	0	...	...	2.4	117.2	2.5	15.2	1.8	14.20
	0	0.9	0.5	0.4	0.5	...	...	0	0	0.3	0.4	40.0	4.30
Hoplodermatidae	0	0	0	0	0	0.2	0.9	0	0	0	0	0	0.09
	...	...	...	...	...	0	0	...	...	...	...	...	0
Unknown	0	0	0	0	0	19.7	2.6	0	0	0	0	0	1.86
	...	...	...	...	...		0	...	...	...	...	...	0
Total	13.6	53.4	55.0	36.0	9.1	35.6	104.8	22.0	153.8	32.5	92.3	28.1	53.02
	30.2	65.8	106.8	11.8	14.5	0	16.0	10.0	19.3	7.0	18.7	130.0	35.84
Grand Total	43.8	119.2	161.8	47.8	23.6	35.6	120.8	32.0	173.1	39.5	111.0	158.1	88.86

* The species of Uroobovella cannot be listed separately in this table. It is almost impossible to preserve and count all the individuals present; some are destroyed and lost; but the total count is approximately correct.

the writers, each type being given in connection with the particular season when it occurs in maximum numbers:

    Spring: Zercon, Macrocheles adults.

    Summer: Chondronema, Macrocheles nymphs, Hoplodermidae.

    Autumn: Histrignathus, Passalacarus, Caelenopsis, hypopi, Zelia.

    Winter: Macrocheles and Seiodes adults, Megisthanus, Zercon.

    All seasons or erratic: Gregarina, Uroseius, Uroobovella, Heterochelytus.

    If the numbers of mites which occur during the colder (October-March)

and warmer (April-September) months are compared rather striking differences are apparent. For the mites which live on the outside of the body of Passalus the average number per individual is 48.8 during the cold season and 59.8 during the warm season; for those that live beneath the wings the figures are 61.4 and 12.5. The only genera of mites for which similar comparisons can be made are Uroobovella (colder season 30.8, warmer season 29.2), Zercon (colder season 50.0, warmer season 9.0), Uroseius (colder season 4.6, warmer season 5.2), and Heterochelytus (colder season 5.9, warmer season 5.0). The subelytral mite Zercon is more than ten times as abundant during the colder months, but the other mite (Heterochelytus) that lives in the same habitat shows little difference and the same is true for the two external mites.

GENERAL CONSIDERATIONS

Passalus cornutus is a beetle of large size. This is probably due to genetic constitution and has been brought about perhaps after evolution through gradual adaptation to a practically unlimited food supply and a stable habitat in rotting logs. Large animals are often vegetarians. By eating wood and the organisms associated with wood Passalus has the advantage of a food resource that is not much sought by other animals and thus avoids competition. Many insects which depend upon wood and the organisms associated with it have become specialists. Some eat wood itself, and probably represent a primitive stage in the utilization of wood as food; others eat wood with the fungi and other organisms that live in it; others raise fungus gardens on beds in which vegetation is the chief ingredient and some (attid ants) can subsist on nothing else; others eat wood and depend on protozoans, which in turn subsist on it in their enterons for food. Passalus is not very specialized in its adaptations for feeding. As an adult it can live, apparently indefinitely, on rotten wood which has been sterilized by heat to kill protozoa and fungi. Large larvae can do the same, but those just hatched apparently require something more. The young larvae will live for a few days when fed on hard, sterilized rotten wood but flourish better if the wood is finely divided and still better if it has been chewed and partially digested or converted into frass by adult beetles. Passalus is on the road to specialization in its feeding adaptations, but it has not gone far. It prefers logs of certain types of trees and rarely or never lives in others; it eats wood and relishes intermixed fungi, but can get along pretty well without the latter; it has no dependence on wood-digesting protozoans.

Large animals are more often sought by commensals, parasites, and symbionts than small. Perhaps the large size of Passalus has been responsible in part for the numerous and varied animals which have become regularly or accidentally associated with it. The fact that Passalus is colonial and has a

home which permits a certain degree of time-binding has doubtless contributed. The comparative stability of its environment has also been a factor. Passalus, among insects, is a large, slow, stupid, vegetarian, which can always be found in the same sort of a place and continues there for long periods of time. Small wonder that sixteen or more small animals have become associated with it. It may be profitable to consider briefly how and why such associations have come about.

There is not general agreement among biologists as to what a parasite, a commensal, or a symbiont is, but everyone will agree that all these are usually small plants or animals which are more or less regularly associated with one or more types of larger plants or animals (hosts) from which they receive some degree of benefit. They may show more or less adaptation to particular hosts; a dog flea or a castor bean tick may feed from many types of mammals, but a Texas fever tick will usually suck blood from nothing but cattle and a beef tapeworm will live in no definitive host but man. Often parasites do some degree of injury and take food from their hosts; commensals are innocuous guests; symbionts benefit their hosts in return for favors received. But there are many vague, confusing associations and exceptions. *Entamoeba histolytica* Schaudinn is a proper parasite of man which produces ulcers in the wall of the intestine and may cause dysentery and death. There is no doubt that it takes food, because it may be seen to engulf red blood corpuscles, and it certainly does injury. But some human hosts carry this amoeba for years without any apparent ill effects. In these this parasite is apparently a harmless commensal.

In Passalus *Chondronema passali* (Leidy) is doubtless a parasite and it is so called by Christie and Chitwood (1931) in their fine paper which describes the habits, anatomy, and life history of this nematode; yet it cannot be very injurious, for a Passalus may support thousands in its body cavity and remain strong. Beetles from which the wings have been removed under the binocular microscope show a continuous mass of wriggling nematodes through the transparent nota; yet appear to be vigorous. It is possible that some of the mites associated with Passalus may help their host by eating fungi or by some other beneficial act, perhaps some may be injurious, but at present such relations are unknown. What the present writers have demonstrated is that at least fifteen species of animals are commonly found with this beetle. Why have these particular animals associated with this particular host? The associates are not accidental; they belong to the beetles. Trombiculid mites are common in suitable places in the Duke Forest. They continually crawl over the ground and fallen logs; yet among thousands of mites no trombiculid was found on a Passalus.

It is possible that many species of mites seek logs and beetles for stability. A decaying log habitat is a guarantee against extreme changes in temperature

and desiccation. A beetle because it is a living animal, has a greater degree of stability; it has various regulating mechanisms to keep its body system operating in a steady state. Such a view of association perhaps is supported by the fact that there are ten times as many Zercons under the wings of Passalus in winter as in summer. Another sub-elytral mite, Heterochelytus, occurs in about equal numbers the year round; but this feeble, slow mite is apparently primarily adapted to live under beetles wings and nowhere else; it belongs to a group (Canestriniidae) in which mites are "of very small size and parasitic on insects" (Banks, 1915). On the other hand a Zercon is a rather speedy runner and may easily migrate from a beetle to the wood in a burrow and back again. Another difference between Zercon and Heterochelytus is that the former probably breeds outside its host, as larvae have not been found on Passalus; whereas those of the latter are often present. On February 17, 1934, masses of frass from three separate Passalus mines were examined for mites. A total of 44 cc. was carefully teased apart and searched with a binocular microscope. The result was 2 Megisthanus, 3 Macrocheles, 2 Zercon, 1 snail, and 1 crane-fly larva. Ewing (1912, 1929) says:

The reasons for the frequent occurrence of parasitism in the Acarina are to be found largely in the minute size, the great abundance, the wide distribution and the diversity of habits of the free living members. Parasitism in a nascent state is seen today in certain living species, as for example *Pediculoides ventricosus*. A single individual of this species may be either predaceous, parasitic, or act as a scavenger. It may be either one of these or all three with equal adaptability depending entirely upon the hazards of its environment.

Most of the mites which live on the outside of the body of Passalus are probably not parasites, but commensals; the essentially sessile uropodids and hypopi get transportation, warmth, and protection. The subelytral mites are probably both parasitic. Zercon imbeds its mouth parts in the soft parts of its host; Heterochelytus has piercing and sucking mouth parts and is a typical sarcoptid.

Nematodes commonly live in decaying organic materials, including logs. Steiner (1932) has discussed the nematodes associated with beetles and says:

From a mere occurrence of the nemas in mines of the bark beetles and their possibly accidental use of the beetles as carriers, the way to true parasitism seems to proceed by the following steps: (1) The use of the bark beetle as an unconditional carrier, (2) the extension of the carrier association into a regular life association under the wing covers or on the exterior surface of the beetle, (3) the production of special cocoons and webs by the nemas on the body of the beetle, (4) the habit of feeding on the beetle itself from the outside (ectoparasitism), and (5) true endoparasitism of nemic larvae.

Of the two nematodes in *Passalus cornutus*, Chondronema is parasitic in the body cavity during its larval development and the adults and eggs are to

be found in rotting wood; Histrignathus lives as an adult in the enteron at the anterior end of the midgut and its eggs are passed out through the anus to develop in rotting wood. Both these are obligate parasites and belong to a group of nematodes which is wholly or largely parasitic. The gregarine which is often attached to the wall of the midgut of Passalus is of course a member of the group Sporozoea, which contains nothing but parasites.

There are several questions which are raised by the study of Passalus which relate to habitat selection as related to parasitism. *Passalus cornutus* prefers oak logs as a habitat. It will be of interest to discover what types of animals are to be found in the logs of different species of trees and what types and species of parasitic animals are associated with insects in logs of various types; i.e. whether various small animals show habitat specificity for particular types of logs and whether the small animals that become associated with animal hosts show the influence of their original log habitat.

SUMMARY

1. The ecology of the beetle, *Passalus cornutus* Fabricius, has been investigated in rotting logs in the Duke Forest.

2. This beetle is colonial, a pair of parents living with a brood of their offspring. Both adults and larvae stridulate, and members of a colony are thus kept together.

3. The food of Passalus consists of rotten wood with its contained organisms. Oak is preferred, but beetles excavate mines in hickory, gum, sourwood, and sometimes even in pine, but will not work in cedar.

4. Adult beetles and well grown larvae will live for weeks in sterilized rotten wood in which all organisms have been killed by heat; but newly hatched larvae, though they will live and grow for a time, will not come to maturity if fed no other food.

5. An adult beetle at 20° C. consumes 0.5 gram of wood per gram of body weight per day.

6. At least sixteen species of animals are found on or in the body of Passalus. These include a gregarine, two nematodes, twelve mites, and a fly. Two of the mites and all the other types of animals are parasites; some of the mites are merely attached to Passalus in order to obtain transportation, protection, and warmth; the relations of others are uncertain.

7. The average number of parasites and commensals found on and within a single Passalus at any time of the year is about 561: protozoans, 1.7; nematodes, 471-6; mites, 88.66; flies, 0.1.

8. Some of the animals associated with Passalus show striking seasonal variations in numbers, in some instances associated with progressive changes in the life history of the host; others are erratic or present more or less uniformly throughout the year.

9. Passalus probably attracts numerous animals because it is large, lives in a rather stable environment to which small animals resort to avoid extreme variations, and because its body furnishes a certain degree of environmental stability for commensals and parasites.

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PARASITES OF CERTAIN NORTH CAROLINA SALIENTIA

By

B. B. BRANDT

Duke University
Durham, N. C.

CONTENTS

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INTRODUCTION

Salientians are often infested with numerous parasites. They, therefore, provide valuable material for the study of the problems of parasitism. The variety of environmental conditions in which amphibians live gives excellent opportunities to study the relationships between parasites and environmental factors. It is remarkable that, although frogs and toads have long been used as material for the study of parasites, there has been no systematic and comprehensive study of the relations of parasitic infestations to the ages, habitats, and habits of hosts. The present paper describes attempts to make such studies on the salientians of North Carolina.

Thanks are due to Dr. A. S. Pearse, under whose direction this study was made and whose patient and helpful criticism rendered its completion possible. Drs. H. E. Ewing and J. Percy Moore identified mites and leeches, respectively. Aid in the study of helminths was given by Drs. G. Steiner, H. A. Baylis, E. W. Price and B. G. Chitwood; and in that of protozoans by Drs. R. R. Kudo and D. L. Hopkins. Dr. L. Stejneger elucidated some difficult questions of host synonymy. Drs. Allen McIntosh, R. Harkema and J. S. Rankin have been of assistance on many occasions. The writer is especially indebted to Mr. George Ross and Miss Mary Shelburne for their untiring efforts in the collection of hosts.

PREVIOUS WORK

The study of North American salientians began with the work of Joseph Leidy in 1851. Before him certain European parasitologists had observed various parasites. Leeuwenhoek (Kudo, 1931) had seen Opalina and Nyctotherus. Other observers of salientian parasites included Goeze (1782), Loschge (1785), Schrank (1788), Zeder (1800), Rudolphi (1801), Creplin (1825), Mehlis (1831), Diesing (1835), and Dujardin (1845). Somewhat later van Beneden (1858), Leuckart (1865), von Linstow (1878) and Looss (1894) made important contributions.

In North America much has been done since Leidy's time. Among many works the following are among the more important. An opalinid was observed in a spadefoot by Stokes (1884). A myxosporidian, *Leptotheca ohlmacheri* (Gurley, 1893), was named in honor of its discoverer, Ohlmacher (1883). Trypanosomes and haemosporidians were found in frogs of the genus Rana and observations were made on the life-histories of the latter (Stebbins, 1904, 1905, 1907). *Nyctotherus parvus* by Walker (1909) and *Entamoeba ranarum* by Craig (1913) were reported from the same host

genus. In 1914 Metcalf began his work on Opalinidae with a description of *Zelleriella antilliensis* and went on to write a monograph (1923) in which he described many new genera, species and forms. *Trichomonas augusta, Hexamitus batrachorum* and *H. ovatus* were studied in the frogs of the western United States (Kofoid and Swezy, 1915; Swezy, 1915, 1916). Hegner (1920, 1921, 1932) recorded blood protozoans and opalinids. The life-history of *Leptotheca ohlmacheri* was studied and *Entamoeba ranarum,* Haemogregarina, *Trypanosoma rotatorium, T. parvum* and Opalina were reported by Kudo (1922). Fortner (1923) studied the frog parasites of the Douglas Lake region reporting Octomitus, Opalina and Nyctotherus. A Trichodina from a toad was described by Fulton (1923). Wenrich (1924, 1932) described an Amphileptus from the gills of tadpoles and reported Retortomonas. Beltran (1925) described an Opalina from a Mexican Hyla. Becker (1925) reported Mastigina from tadpoles. Drbohlav (1925) made observations on the occurrence of Herpetomonas, Leishmania and Trypanosoma in frogs. Tanabe (1925) reported *Karotomorpha bufonis.* Marx (1927) described *Trigonomonas diplostomum.* Sanders (1928) found Karyolysus and Lankesterella in frogs of the genus Rana. Travis (1934) reported Karotomorpha from *Rana pipiens.*

The knowledge of the trematode fauna of North American Salientia has likewise developed tremendously since the work of Leidy. Stiles and Hassall (1894) catalogued the known species. Bensley (1897) recognized two varieties of the so-called *Distomum cygnoides.* Pratt (1900, 1904) presented lists of thirteen and eighteen species respectively. Stafford, in a series of papers from 1900 to 1905, differentiated American trematodes previously confused with those of Europe and described others which were new. Seeley (1906) described *Ostiolum complexus.* Cary (1909) contributed observations on the life-history of *Diplodiscus temperatus.* Cort, in a series of papers from 1912 to 1919, added new species and other information concerning trematodes. Faust (1917) described a larval holostome from frogs. Stunkard (1917) monographed the polystomes and amphistomes. Ward (1918) gave a summary of trematodes from fresh-water hosts. Guberlet (1920) described *Gorgodera circava.* Fortner (1923) reported five species of flukes from the frogs of the Douglas Lake region. Millzner (1924a) described *Megalodiscus ranophilus.* Beaver (1929) reported *Allassostoma parvum* from frogs and determined the life-history of the trematode. Hughes (1929) reported *Diplostomulum vergrandis* from *Rana pipiens.* Irwin (1929) described *Haematoloechus parviplexus.* Hunter (1930, 1932) described *Diplodiscus intermedius* and reported Clinostomum. Miller (1930) gave a careful redescription of *Glypthelmins quieta* and synonymized Margeana with Glypthelmins. Lucker (1931) described *Haplometrana intestinalis.* Harwood (1932) described numerous species of trematodes from the Salientia of Texas.

Ingles (1932, 1932a) described *Cephalogonimus brevicirrus* and several lung flukes. Krull (1930 to 1935) made important contributions, especially in the field of life-histories. Ingles and Langston (1933) described *Gorgoderina multilobata*. Sokoloff and Caballero (1933) and Caballero and Sokoloff (1934) reported the trematode parasites of *Rana montezumae*. Stunkard and Dunihue (1933) reported Leichriorchis. Trowbridge and Hefley (1934) reported several trematodes from Oklahoma Salientia.

Since Leidy reported his *Taenia pulchella*, few cestodes have been observed in North American frogs and toads. Stiles and Hassall (1912) gave a host list for *Taenia dispar* which included *Bufo americanus, B. lentigenosus* and *Rana pipiens*. Jewell (1916) described *Cylindrotaenia americana*, as new genus and species, from *Acris gryllus, Rana pipiens* and *Bufo lentigenosus*. Dickey (1921) described *Distoichometra bufonis*, new genus and species, from *Bufo lentigenosus*. Fortner (1923) reported proteocephalids in *Rana pipiens* and *R. clamitans*. Hannum (1925) described *Ophiotaenia magna* from *Rana catesbeiana*. Osler (1931) described *Ophiotaenia saphena* from *Rana clamitans* and Thomas (1931, 1934) found that infestation resulted from the ingestion of copepods harboring the larval parasites. Harwood (1932) reported *Ophiotaenia magna* from *Rana catesbeiana* and *R. clamitans* and suggested its possible synonymy with *O. filaroides*. The same author reported *Cylindrotaenia americana* from *Acris gryllus, Hyla squirella* and *Pseudacris triseriata*. Trowbridge and Hefley (1934) reported *Ophiotaenia magna* from Bufo, Acris and Rana and *Cylindrotaenia americana* from Acris.

Five nematodes of salientians were catalogued by Stiles and Hassall (1894, 1905). Steiner (1924) described *Oswaldocruzia leidyi* along with several others from *Hyla cinerea*. Walton, in a series of papers from 1927 to 1935, has been most active in increasing the known species of salientian nematodes. Holl (1928) described *Cosmocercoides dukae* which is now known from many hosts. Canavan (1929) described the dioctophymoid, *Eustrongylides wenrichi*, from the bullfrog. Harwood (1930, 1932) has made important contributions. Travassos (1930) discussed the validity of North American species of Rhabdias. Trowbridge and Hefley (1934) reported numerous nematodes from Oklahoma Salientia.

Acanthocephala are rarely referred to in the literature relating to North American salientian parasites. Millzner (1924) described the larval *Centrorhynchus californicus* from *Hyla regilla*. Sandground (1926) has reported *Moniliformis moniliformis* from *Bufo marinus* in Honduras.

Leeches, as temporary parasites of frogs, have been reported by Nachtrieb, Hemingway and Moore (1912) and by Moore (1918).

Lernaea, a parasitic genus of Crustacea, has been found on frogs by Stunkard and Cable (1931). Shannon (1915) observed a mosquito, *Culex territans*, feeding on frogs. Darling (1910) reported the tick, *Amblyomma*

varium from *Bufo marinus* in Panama. Hooker, Bishopp and Wood (1912) reported *A. dissimile* from Bufo in Texas, Mexico, Jamaica and Panama and *A. cajennense* in a Texas Bufo. Ewing (1925) described *Hannemania hylae* from *Hyla arenicolor* and (1931) *H. penetrans* from Rana. Hubert (1927) reported a mite from *Rana sphenocephala* in Louisiana.

Relatively little work on the ecology of salientian parasites has been published. Ward (1909) reported that his student, Duncanson, had found fewest parasites in *Rana pipiens* just after spawning and that there was an increase through the following months to a maximum at hibernation. Cary (1909) studied the life-cycle of *Diplodiscus temperatus* and found that the cercariae encysted on stones and water-plants and were then ingested by tadpoles. Metcalf, in his monograph (1923) and in subsequent briefer papers, studied the opalinid parasites and advanced opinions concerning the origin and distribution of the families of Salientia. Noble (1925) has disagreed with Metcalf's conclusions. Fortner (1923), in a study of frog parasites in the Douglas Lake region of Michigan, found a variation in the parasites of frogs from different habitats. Trypanosomes were found by Hegner (1929) to occur in aquatic but not in terrestrial newts. These flagellates in Europe are transmitted by a leech (Franca, 1908). Noller (1913) reported a similar vector for Lankesterella in the same region. In America, Miss Sanders (1928) believes that Karyolysus is not transmitted by a leech but by a vector which attacks frogs only after metamorphosis.

Krull, in a series of papers from 1930 to 1934, found that frogs acquired certain lung flukes by ingesting Odonata infested with metacercariae and that they annually lost and renewed their infestations. The same author (1935) worked out the life-history of *Halipegus occidualis.* Krull and Price (1932) found that frogs became infested with *Diplodiscus temperatus* by swallowing their molted skins, on which the metacercariae had encysted. Frogs were found to serve as intermediate hosts for *Zeugorchis syntomentera* and *Alaria mustelae* by Ingles (1933a) and Bosma (1934), respectively. Ingles (1933) studied the life-history of *Ostiolum oxyorchis* and was able to synonymize *O. confusus* with it. The infestation of frogs with *Ophiotaenia saphena* by ingesting infested copepods was discovered by Thomas (1931, 1934). Joyeux (1924) states that *Cylindrotaenia americana* is capable of direct development in a single host.

Walton (1929) found that the larvae of *Rhabdias ranae* may reach the infective stage before being voided from the rectum of the host. The first larval stage of *Cosmocercoides dukae* was found to be free living and the second larval stage to be infective (Harwood, 1930). Working on the salamanders of Japan, Pearse (1932) found a significant seasonal variation in certain parasites. Trematodes and acanthocephalans were found only in acquatic hosts. Holl (1932) reported seasonal variations in parasites of Triturus and Acris and that habitat influenced the parasitic fauna.

Locality Studied

Beaufort County, where all the writer's collecting was done, is in the east central part of North Carolina. It is located on the low-lying marine terraces of the Atlantic Coastal Plain and is generally level, with gently rolling areas near many of the streams, especially in the western end of the county. A benchmark on the courthouse at Washington, the county seat, records an altitude of about six feet above sea level. The drainage of the county varies with the topography, is generally poor, and is through the Pamlico and Pungo rivers and their tributaries. The soils consist chiefly of sands, sandy loams, muck and peat.

The climate of Beaufort County is mild. The mean annual temperature is 16.7° C. Killing frosts seldom occur after the first week in April or before the last of October. The mean annual rainfall of 145 cm. is well distributed throughout the year. The winters are generally mild, the average temperature for December, January and February being 7.4° C. The summer months, June, July and August, have an average temperature of 25.8° C. (Cobb, Vanatta, Brinkley, and McDowell, 1919).

Methods of Investigation

The hosts were collected by hand, usually at night with the aid of an electric flash-light. Hibernating individuals were obtained by digging in favorable places for terrestrial species and by probing under submerged ledges for those with aquatic habits. Species active in winter could best be procured on warm rainy nights along highways. Since all the salientians studied were taken in Beaufort County and examinations were made at Duke University, a delay of from one to several days between collections and examinations was unavoidable. On this account, data regarding food habits are meagre. The animals were examined for parasites externally and internally under a binocular microscope. The parasites were removed, counted and either studied alive or prepared for permanent mounts.

Smears of intestinal contents, blood, kidneys and other organs were examined under the compound microscope for smaller protozoan parasites. Permanent preparations of blood protozoans were made by fixating with 95 per cent alcohol and treating with Giemsa's stain. Other protozoans were fixed in Schaudinn's fluid and stained with iron-hematoxylin and occasionally counterstained with eosin.

Trematodes were washed in normal saline, relaxed in tap water, fixed with Conant's fluid or Bouin's fluid, stained with Grenacher's borax-carmine, Ehrlich's hematoxylin or cochineal, and mounted in damar. Some of the worms were serially sectioned but most of them were preserved as toto mounts. Sections were stained with Ehrlich's hematoxylin using eosin as a counterstain.

Cestodes were treated in the same manner as trematodes. Some of the cylindrical worms were pressed flat between glass plates before fixation in order to facilitate study of toto mounts. Serial sections were also prepared.

Nematodes were washed in normal saline then either relaxed in tap water or fixed at once in 70 per cent alcohol. The worms were stored in the latter fluid and mounted for study in glycerine, lacto-phenol or creosote.

Acanthocephalans were treated in the same manner as trematodes.

Leeches were preserved in 10 per cent formalin.

Mites were fixed in Conant's fluid or were mounted directly in Berlese's medium (Lee, 1928, p. 514).

HOSTS EXAMINED

Twenty-six species of Salientia are known to occur in North Carolina. Of these twenty-two have been found in Beaufort County. After four months of preliminary examinations, six species were selected for study through a complete annual cycle. These had been found in an earlier study (Brandt, 1936) to be available at all seasons of the year. In respect to habitats they may be classified into a series as aquatic, semi-aquatic, palustrine, terrestrial, fossorial and arboreal species. The original plan involved the examination of five individuals of each host species in each month of the year and this schedule was adhered to as closely as possible. All of the animals used were taken in Beaufort County.

Aquatic Species: *Rana catesbeiana* Shaw 1802

The bullfrog is the most completely aquatic species of the region. Its range includes "North America east of the Rocky Mountains except the extreme southeast and Gulf states coastal plain" (Stejneger and Barbour, 1933). In North Carolina, Brimley (1926) gives the range as statewide. The species is active to some extent in every month of the year but most large individuals hibernate. By dint of careful search it was possible to procure fourteen hibernating individuals of large size for the winter examinations. Only very small individuals were observed to be active during the winter of 1934-35. In Beaufort County the species has been observed to breed in April and May. Because there was a considerable difference in the number of parasites found in large and in small bullfrogs, it seemed desirable to separate the group into two series, large and small. The length, 100 mm., represents the minimum breeding size (Wright, 1931), and was therefore selected as the point of division. The lengths of the thirty-three large bullfrogs examined average 142.3 mm. The extreme lengths were 100.0 mm. and 175.0 mm. The thirty-eight small bullfrogs average 44.9 mm. in length. The extreme lengths were 32.6 mm. and 82.5 mm. The entire series of seventy-one bullfrogs averaged 90.1 mm. in length. Since the bullfrog is never very numerous in a single restricted locality, it was necessary to take hosts from numerous localities. The con-

tents of the enterons of the hosts consisted of crayfish (27.7%), sand (19.7%), insects (17.8%), molted skins (16.0%), debris (9.8%), snails (5.3%), and small frogs (3.7%). The seasonal distribution of hosts is shown in Table 1.

Semi-aquatic Species: *Rana sphenocephala* (Cope, 1886)

The southern leopard-frog is distinctly less aquatic than the cogeneric bullfrog, but it spends much time in and near the water. Stejneger and Barbour (1933) give "southeastern states" as the range of the species. Brimley (1926) gives the range in North Carolina as "eastern district." This includes all of the coastal plain and portions of the Piedmont region. The great abundance of the species permitted the procuring of five mature individuals each month from a certain small pond. The lengths of these animals averaged 55.1 mm. The extremes measured 40.6 mm. and 73.6 mm. in length. The enterons of the hosts contained molted skins (59.0%), debris (16.7%), insects (8.9%), spiders (5.9%), earthworms (.83%), and myriapods (.40%). The seasonal distribution of hosts is shown in Table 1.

Terrestrial Species: *Bufo fowleri* Hinckley 1882

Fowler's toad is characteristically terrestrial. However, it visits an aquatic environment for about two months of the year when breeding. The range is "New England and New York, southward to Georgia, west to Michigan and Missouri, but occurring also on the Atlantic and Gulf coastal plain to central Texas. (Not known in peninsular Florida)" (Stejneger and Barbour, 1933). The range in North Carolina is statewide (Brimley, 1926). During the winter it was necessary to dig out individuals hibernating under heaps of litter. The sixty-two hosts examined averaged 48.5 mm. in length. The extreme lengths were 30.9 mm. and 64.0 mm. The enterons of the animals examined contained sand (36.3%), molted skins (30.6%), debris (22.8%), and insects (10.3%). The seasonal distribution of hosts is shown in Table 1.

Fossorial Species: *Scaphiopus holbrookii* (Harlan, 1835)

The spadefoot is more distinctly terrestrial than Fowler's toad. The time spent in an aquatic environment when breeding is always limited and has been stated to be restricted in some years to a single day Hibernating animals were dug from a depth of about six inches in well drained, sandy areas. The range of the spadefoot includes "eastern states, Massachusetts to Florida, west to Louisiana, Texas to Arkansas" (Stejneger and Barbour, 1933). The range in North Carolina includes Wake, Carteret, Henderson, Beaufort, Pitt, Greene, Wilson, Nash and Columbus counties (Brandt, 1936). The average length of the individuals examined was 51.0 mm. The extremes in length were 23.5 mm. and 67.0 mm. The enterons of the hosts examined contained

insects (41.4%), sand (36.4%), debris (12.3%), myriapods (5.9%), snails (3.0%), spiders (0.6%), and seeds (0.4%). The seasonal distribution of hosts is shown in Table 1.

Palustrine Species: *Pseudacris brimleyi* Brandt and Walker 1933

This chorus frog was selected as the representative of an arboreal form which has reverted to terrestrial life. It is of especial interest in comparison with its more arboreal relative of similar size, *Hyla crucifer*. About four months are spent at the breeding pools; the remainder of the year this species usually spends along swampy shores. The known range (Brandt and Walker, 1933) includes "southern Virginia to Northern Georgia, along the coast" In North Carolina it is known from Beaufort, Pitt, Greene, Craven, Edgecombe and Wilson counties (Brandt, 1936). The fifty-five hosts averaged 27.4 mm. in length. The extreme lengths were 19.9 mm. and 34.3 mm. The enterons of the animals contained insects (75.0%), spiders (16.7%), and debris (8.3%). The seasonal distribution of hosts is shown in Table 1.

Arboreal Species: *Hyla crucifer* Wied 1838

The spring-peeper is the most arboreal of the species in the series studied. About four months exposure to an aquatic environment occurs at the breeding season. The range of *Hyla crucifer* includes "New Brunswick to Manitoba, south to Georgia, Louisiana, Arkansas and Kansas" (Stejneger and Barbour, 1933). In North Carolina, the range is statewide (Brimley, 1926). The sixty hosts examined averaged 26.4 mm. in length. The extremes in length were 14.9 mm. and 33.0 mm. The enterons contained insects (57.6%), debris (20.6%), molted skins (16.6%) and sand (5.2%). The seasonal distribution of hosts is shown in Table 1.

PARASITES OF HOSTS EXAMINED

In the following section is given a list of parasites found in the six species of hosts during the annual cycle from March, 1934 to March, 1935. Following the name of each parasite there may be one or two numbers. The first indicates the percentage infestation and the second, when present, indicates the average number of parasites per host. Finally, the part of the host's body infested is given.

Rana catesbeiana (Over 100 mm. Long)

The thirty-three large bullfrogs examined contained the following parasites:

Protozoa

Cytamoeba bactifera Labbe 1894; 6.06%; erythrocytes

Entamoeba ranarum Grassi 1879; 3.03%; intestine

Unidentified cysts; 42.4%; muscles

Karyolysus sp. or *Lankesterella* sp.; 24.2%; blood
Leptotheca ohlmacheri (Gurley 1893); 3.03%; kidney
Nyctotherus cordiformis (Ehrenberg 1838); 9.1%; intestine
Octomitus intestinalis Prowazek 1904; 84.8%; intestine
Trichomonas augusta Alexeieff 1911; 97.0%; intestine
Trypanosoma rotatorium (Mayer 1843); 9.1%; blood

Trematoda

Diplodiscus temperatus Stafford 1905; 24.3%; 0.85%; rectum
D. intermedius Hunter 1930; 54.6%; 6.2; rectum
All *Diplodiscus;* 72.8%; 7.3; rectum
Glypthelmins subtropica Harwood 1932; 54.6%; 4.03; intestine
Gorgodera amplicava Looss 1899; 63.8%; 8.4; urinary bladder
Gorgoderina attenuata (Stafford 1902); 9.1%; 1.64; kidney and bladder
All *Gorgoderinae;* 69.7%; 10.0; kidney and urinary bladder
Haematoloechus sp.; 18.2%; 0.27; lungs
H. breviplexus Stafford 1902; 33.3%; 1.67; lungs
H. longiplexus Stafford 1903; 9.1%; 0.15; lungs
Loxogenes bicolor Krull 1933; 36.4%; 1.49; pancreas and liver
Encysted flukes; 75.7%; 22.8; general

Cestoda

Ophiotaenia saphena Osler 1931; 9.1%; 0.091; intestine
Proteocephalid cysts; 42.4%; 32.5; general

Nematoda

Agamascaris odontocephala Steiner 1924; 42.4%; .697; body cavity
Agamonema cysts; 90.9%; 127.2; general
Cosmocercoides dukae (Holl 1928); 12.1%; 1.24; intestine
Dujardinia sp.; 21.2%; 0.76; body cavity
Foleyella americana Walton 1929; 3.03%; 0.06; body cavity
F. ranae Walton 1929; 51.6%; 3.64; body cavity
Microfilaria sp.; 30.3%; blood
Oswaldocruzia pipiens Walton 1929; 9.1%; 0.121; intestine
Oxysomatium longicaudata (Walton 1929); 24.3%; 6.22; enteron
Physaloptera sp.; 42.4%; 1.69; stomach
Rhabdias sp.; 3.03%; 0.06; body cavity
R. ranae Walton 1929; 12.1%; 0.18; lungs
Spironoura catesbeianae (Walton 1929); 45.5%; 28.0; intestine
Spiroxys sp.; 9.1%; 0.70; enteron

Acanthocephala

Centrorhynchus sp.; 81.8%; 13.9; body cavity

Hirudinea

Macrobdella ditetra Moore undescribed; 12.1%; 0.303; external

Acarina

Hannemania penetrans Ewing 1931; 12.1%; 0.243; skin

Rana catesbeiana (UNDER 100 MM. LONG)

The thirty-eight small bullfrogs examined contained the following parasites:

Protozoa

Entamoeba ranarum Grassi 1879; 13.2%; intestine
Karyolysus sp. or *Lankesterella* sp.; 5.25%; blood
Leptotheca ohlmacheri (Gurley 1893); 34.2%; kidney
Octomitus intestinalis Prowazek 1904; 97.4%; intestine
Trichomonas augusta Alexeieff 1911; 73.7%; intestine
Trypanosoma rotatorium (Mayer 1843); 10.5%; blood
Unidentified flagellate; 10.5%; intestine

Trematoda

Diplodiscus temperatus Stafford 1905; 36.8%; 1.53; rectum
D. intermedius Hunter 1930; 7.91%; 0.263; rectum
All *Diplodiscus;* 47.3%; 1.84; rectum
Glypthelmins subtropica Harwood 1932; 2.63%; 0.395; intestine
Gorgodera amplicava Looss 1899; 2.63%; 0.0263; urinary bladder
Gorgoderina attenuata (Stafford 1902); 5.25%; 0.132; urinary bladder
All bladder flukes; 7.9%; 0.158; urinary bladder
Haematoloechus breviplexus Stafford 1902; 10.5%; 0.105; lungs
H. longiplexus Stafford 1902; 5.25%; 0.0525; lungs
All *Haematoloechus;* 18.4%; 0.42; lungs
Loxogenes bicolor Krull 1933; 44.7%; 0.947; pancrea and liver
Larval flukes; 63.2%; 6.72; general

Cestoda

Proteocephalid cysts; 42.2%; 3.58; general

Nematoda

Agamascaris odontocephala Steiner 1924; 2.63%; 0.0263; body cavity
Agamonema sp.; 18.4%; 0.474; general
Cosmocercoides dukae (Holl 1928); 2.63%; 0.0263; intestine
Foleyella americana Walton 1929; 2.63%; 0.0263; body cavity
Oswaldocruzia pipiens Walton 1929; 18.4%; 0.342; intestine
Spironoura catesbeianae (Walton 1929); 2.63%; 0.0263; intestine
Rhabdias sp.; 21.1%; 0.474; body cavity
R. ranae Walton 1929; 15.8%; 0.237; lungs

Acanthocephala

Centrorhynchus sp.; 5.25% ; 0.132; body cavity

Hirudinea

Macrobdella ditetra Moore undescribed; 5.25% ; 0.079; external

Rana sphenocephala

The sixty *Rana sphenocephala* examined were infested with the following parasites:

Protozoa

Cytamoeba bacterifera Labbe 1894; 40.0% ; erythrocytes
Entamoeba ranarum Grassi 1879; 1.67% ; intestine
Karyolysus sp. or *Lankesterella* sp.; 28.3% ; blood
Leptotheca ohlmacheri (Gurley 1893) ; 10.0% ; kidney
Nyctotherus cordiformis (Ehrenberg 1838) ; 13.3% ; intestine
Octomitus intestinalis Prowazek 1904; 90.0% ; intestine
Opalina sp.; 1.67; intestine
O. carolinensis Metcalf 1923; 20.0% ; intestine
O. kennicotti Metcalf 1923; 1.67% ; intestine
O. obtrigonoidea Metcalf 1923; 15.0% ; intestine
All *Opalina;* 30.0% ; intestine
Trypanosoma rotatorium (Mayer 1843) ; 38.3% ; blood
Trichomonas augusta Alexeieff 1911; 78.4% ; intestine
Unidentified flagellate; 10.0% ; intestine

Trematoda

Brachycoelium hospitale (Stafford 1900) ; 3.33% ; 0.216; intestine
Cephalogonimus americanus Stafford 1902; 1.67% ; 0.0167; intestine
Diplodiscus temperatus Stafford 1905; 40.0% ; 0.867; rectum
Gorgoderina attenuata (Stafford 1902) ; 5.0% ; 0.083; urinary bladder
Loxogenes bicolor Krull 1933; 5.0% ; 0.01; pancreas and liver
Ostiolum complexus (Seeley 1906) ; 56.7% ; 5.72; lungs
Larval flukes; 53.5% ; 37.8; general

Cestoda

Proteocephalid cysts; 51.7% ; 10.1; general

Nematoda

Agamascaris odontocephala Steiner 1924; 16.7% ; 0.467; body cavity
Agamonema sp.; 63.3% ; 4.16; general
Cosmocercoides dukae (Holl 1928) ; 3.33% ; 0.083; intestine
Dujardinia sp.; 5.0% ; 0.117; body cavity
Foleyella sp.; 1.67% ; 0.033; body cavity
F. americana Walton 1929; 23.7% ; 0.733; body cavity

F. ranae Walton 1929; 11.7% ; 0.267 ; body cavity
All *Foleyella;* 35.0% ; 1.033 ; body cavity
Microfilaria sp.; 6.67% ; blood
Oswaldocruzia pipiens Walton 1929; 48.3% ; 2.18 intestine
Rhabdias sp.; 58.3% ; 8.78 ; body cavity
R. ranae Walton 1929 ; 48.3 ; 2.48 ; lungs

Acanthocephala
Centrorhynchus sp.; 28.3% ; 2.62 ; body cavity

Acarina
Hannemania penetrans Ewing 1931 ; 6.67% ; 0.10 ; skin

Bufo fowleri
The sixty-two *Bufo fowleri* examined contained the following parasites:

Protozoa
Nyctotherus cordiformis (Ehrenberg 1838) ; 35.5% ; intestine
Octomitus intestinalis Prowazek 1904 ; 53.2% ; intestine
Opalina sp.; 1.61% ; intestine
O. obtrigonoidea Metcalf 1923 ; 20.9% ; intestine
O. triangulata Metcalf 1923 ; 1.61% ; intestine
O. virguloidea Metcalf 1923 ; 6.45% ; intestine
Trichomonas augusta Alexeieff 1911 ; 93.5% ; intestine
Trypanosoma rotatorium (Mayer 1843) ; 3.21% ; blood

Trematoda
Brachycoelium hospitale (Stafford 1900) ; 1.61% ; 0.016 ; intestine
Gorgodera amplicava Looss 1899 ; 1.61% ; 0.016 ; urinary bladder
Gorgoderina attenuata (Stafford 1902) ; 3.21% ; 0.065 ; urinary bladder
G. simplex (Stafford 1902) ; 1.61% ; 0.016 ; urinary bladder
G. translucida (Stafford 1902) ; 1.61% ; 0.032 ; urinary bladder
All bladder flukes ; 8.07% ; 0.129 ; urinary bladder
Larval flukes ; 21.0% ; 0.581 ; general

Cestoda
Distoichometra bufonis Dickey 1921 ; 40.3% ; 1.97 ; enteron
Proteocephalid cysts ; 3.21% ; 1.61 ; general

Nematoda
Agamonema sp.; 42.5% ; 15.8 ; general
Cosmocercoides dukae (Holl 1928) ; 30.7% ; 0.483 ; intestine
Oswaldocruzia pipiens Walton 1929 ; 61.3% ; 3.5 ; intestine
Physaloptera sp.; 1.61% ; 0.0161 ; stomach
Rhabdias sp.; 1.61% ; 0.032 ; body cavity
R. ranae Walton 1929 ; 1.61% ; 0.0483 ; lungs

Acanthocephala

Centrorhynchus sp.; 1.61% ; 0.0161 ; body cavity

Acarina

Hannemania penetrans Ewing 1931 ; 4.83% ; 0.145 ; skin

Scaphiopus holbrookii

The sixty *Scaphiopus holbrookii* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838) ; 58.3% ; intestine
Octomitus intestinalis Prowazek 1904 ; 61.8% ; intestine
Opalina carolinensis Metcalf 1923 ; 1.67% ; intestine
O. oblanceolata Metcalf 1923 ; 10.0% ; intestine
O. obtrigonoidea Metcalf 1923 ; 10.0% ; intestine
O. triangulata Metcalf 1923 ; 6.7% ; intestine
Trichomonas augusta Alexeieff 1911 ; 76.4% ; intestine

Cestoda

Distoichometra bufonis Dickey 1921 ; 16.7% ; 0.92 ; enteron
Proteocephalid cysts ; 1.7% ; 0.33 ; intestinal wall

Nematoda

Agamonema sp.; 26.7% ; 5.62 ; general
Cosmocercoides dukae (Holl 1928) ; 71.7% ; 10.0 ; intestine
Oswaldocruzia leidyi Travassos 1917 ; 13.3% ; 0.23 ; intestine
O. pipiens Walton 1929 ; 38.3% ; 1.52 ; intestine
Physaloptera sp.; 3.3% ; 0.20 ; stomach
Rhabdias sp.; 1.7% ; 0.017 ; body cavity
R. ranae Walton 1929 ; 1.7% ; 0.017 lungs

Pseudacris brimleyi

The fifty-five *Pseudacris brimleyi* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838) ; 30.9% ; intestine
Octomitus intestinalis Prowazek 1904 ; 56.3% ; intestine
Opalina chorophili Metcalf 1923 ; 45.5% ; intestine
O. hylaxena Metcalf 1923 ; 1.8% ; intestine
O. oblanceolata Metcalf 1923 ; 1.8% ; intestine
O. obtrigonoidea Metcalf 1923 ; 9.1% ; intestine
O. pickeringii Metcalf 1923 ; 16.4% ; intestine
O. virguloidea Metcalf 1923 ; 12.7 ; intestine

Trichomonas augusta Alexeieff 1911 ; 30.9% ; intestine
Trypanosoma rotatorium (Mayer 1843) ; 1.8% ; blood
Unidentified flagellate ; 1.8% ; intestine

Trematoda

Brachycoelium hospitale (Stafford 1900) ; 72.8% ; 6.69 ; intestine
Diplodiscus temperatus Stafford 1905 ; 5.5% ; 0.055 ; rectum
Larval flukes ; 3.6% ; 2.36 ; general

Nematoda

Agamascaris odontocephala Steiner 1924 ; 1.8% ; 0.018 ; body cavity
Agamonema sp. ; 9.1% ; 0.47 ; general
Cosmocercoides dukae (Holl 1928) ; 78.2% ; 2.64 ; intestine
Oswaldocruzia pipiens Walton 1929 ; 40.0% ; 1.05 ; intestine
Physaloptera sp. ; 3.6% ; 0.092 ; stomach
Rhabdias sp. ; 18.2% ; 0.38 ; body cavity
Rhabdias ranae Walton 1929 ; 41.8% ; 0.80 ; lungs

Acanthocephala

Centrorhynchus sp. ; 7.3% ; 0.127 ; body cavity

Hyla crucifer

The sixty *Hyla crucifer* examined contained the following parasites:

Protozoa

Nyctotherus cordiformis (Ehrenberg 1838) ; 43.3% ; intestine
Octomitus intestinalis Prowazek 1904 ; 66.7% ; intestine
Opalina sp. ; 6.67% ; intestine
O. chorophili Metcalf 1923 ; 5.0% ; intestine
O. hylaxena Metcalf 1923 ; 5.0% ; intestine
O. obtrigonoidea Metcalf 1923 ; 21.7% ; intestine
O. pickeringii Metcalf 1923 ; 48.3% ; intestine
O. virguloidea Metcalf 1923 ; 5.0% ; intestine
Trichomonas augusta Alexeieff 1911 ; 65.0% ; intestine
Trypanosoma rotatorium (Mayer 1843) ; blood

Trematoda

Brachycoelium hospitale (Stafford 1900) ; 6.67% ; 0.167 ; intestine
Diplodiscus temperatus Stafford 1905 ; 3.33% ; 0.033 ; rectum
Glypthelmins sp.; 18.3% ; 1.82 ; intestine
Larval flukes ; 3.33% ; 0.033 ; general

Cestoda

Proteocephalid cysts ; 3.33% ; 0.134 ; general

Nematoda

Agamascaris odontocephala Steiner 1924; 1.67%; 0.0167; body cavity
Agamonema sp.; 25.0%; 7.48; general
Cosmocercoides dukae (Holl 1928); 13.4%; 0.167; intestine
Oswaldocruzia pipiens Walton 1929; 8.33%; 0.55; intestine
Physaloptera sp.; 3.33%; 0.067; stomach
Rhabdias sp.; 1.67%; 0.05; body cavity
R. ranae Walton 1929; 3.33%; 0.083; lungs

Acanthocephala

Centrorhynchus sp.; 1.67%; 0.0167; body cavity

SEASONAL VARIATION

Tables 7 to 13 present the data concerning seasonal variation of the parasites of the hosts examined. The groupings used, rather than the tabulation by months, were selected in order to increase the size of the groups thus increasing the statistical reliability of the data.

Study of these tables indicates that much of the variation shown is not particularly significant. This is true of the protozoans infesting the intestine. The blood protozoans, however, appeared to exhibit a significant seasonal variation. Trypanosomes were more common in Rana during the warmer periods of the year. They were found in *Bufo fowleri* in August, in *Hyla crucifer* from December to May, and once in *Pseudacris brimleyi* in October. The haemosporidians, Karyolysus and Lankesterella, were more common in the warmer part of the year. Cytamoeba was more prevalent in the colder part of the year.

Lung flukes were less abundant at the breeding season of *Rana catesbeiana* and *R. sphenocephala*. The large bullfrogs had most bladder flukes in the summer and fewest in February. *Rana sphenocephala* had, however, its maximum infestation in February. *Bufo fowleri* harbored most bladder flukes in late summer and autumn.

Flukes of the genus Diplodiscus were very variable in the small bullfrogs but in the large individuals the parasite is most common at hibernation and least common at the breeding season. *Rana sphenocephala* harbors few Diplodiscus in spring, many in August, and fewer thereafter. These parasites were rare or absent in other hosts.

Brachycoelium hospitale was present in *Hyla cricufer* during the breeding season and shortly thereafter. The highest infestation in *Pseudacris brimleyi* occurred at about the breeding season and the lowest occurred in midsummer. This parasite was rare in *Rana sphenocephala* and was found only in the first half of the year.

Encysted trematodes occurred in all hosts except the spadefoot. Their frequency in *Bufo fowleri* and the large *Rana catesbeiana* appeared haphazard.

In *Hyla crucifer* there was one in each February and May. They were similarly rare in *Pseudacris brimleyi*. *Rana sphenocephala* showed a less infestation at the breeding season and more during the succeeding months.

Loxogenes bicolor showed a rather constant frequency in large bullfrogs but was absent late in the period of hibernation. The occurrence of this fluke was more variable in small bullfrogs and showed a maximum in early summer. *Rana sphenocephala* harbored few of the parasites, with the greatest incidence in May.

In the large bullfrogs mature cestodes were found only during a brief period after breeding. They were found only in the large *Rana catesbeiana*, *Bufo fowleri* and *Scaphiopus holbrookii*. Proteocephalid cysts occurred in all species except *Pseudacris brimleyi*. They tended to be more frequent after the hosts had visited an aquatic environment.

Bufo fowleri contained more Oswaldocruzia in midsummer; *Scaphiopus holbrookii* had a maximum infestation in March with a gradual decrease thereafter; *Hyla crucifer* harbored more of the parasites early in the winter; and *Pseudacris brimleyi* exhibited its greatest percentage of infestation later in the winter. *Rana sphenocephala* harbored more Oswaldocruzia at the breeding season and least in midsummer. The small bullfrogs harbored more of these parasites in March, while the large bullfrogs contained them chiefly at the breeding season.

Foleyella in the large bullfrogs, showed a minimum in July and a maximum in December. The small bullfrogs had but a single infestation. *Rana sphenocephala* had fewer of the parasites at and just after breeding and more in early winter. Microfilaria were most common early during the hibernation of the large *Rana catesbeiana* and least common at the breeding season. *R. sphenocephala* also harbored them less frequently at the breeding season. The maximum infestation occurred early in winter.

Rhabdias, in the large bullfrogs, became more prevalent through the summer and early autumn. Small bullfrogs harbored more in August and least in May. *Rana sphenocephala* showed its highest infestation in February and least in May. In *Pseudacris brimleyi*, this parasite was most frequent in March and least so in August. Rhabdias was rare in the other hosts.

Cosmocercoides occurred in all species of hosts studied. The parasite appeared to be more abundant at about the time of breeding.

The larval acanthocephalan, Centrorhynchus, was more common in *Rana sphenocephala* at the breeding season. The large bullfrogs tended toward constancy in percentage of infestation but more individuals harbored the parasites during hibernation. Infestation was uncommon in the other hosts studied.

Macrobdella ditetra was found only in midsummer on bullfrogs and not on other hosts. *Hannemania penetrans* was found on the toad and on the large

bullfrogs only in summer. *Rana sphenocephala* showed a greater infestation by this mite in May and less in late summer.

DISCUSSION

The Salientia are of especial interest to a parasitologist. They possess a considerable degree of general similarity yet show a range of habitats, sizes, and habits which profoundly influence their parasitic faunas. They support a wide variety of parasites. The small size of salientians makes them comparatively easy to examine. Their recognized value has led to their extensive use as laboratory animals in the teaching of parasitology. They have not received adequate recognition as material for the investigation of the fundamental problems of the ecology of parasites. Those of North Carolina provide excellent material for the study of ecological problems related to parasitism. The eastern district of the state is inhabited by twenty-four species of frogs and toads. These live in habitats ranging from aquatic to those which are more or less completely terrestrial, fossorial, and arboreal. Parasites often occur in great variety and large numbers. The mild climate permits many species of hosts to remain active for the greater part of the winter. Opportunity is offered to make interesting comparisons of the effect of habitat on parasites, of seasonal variation, host specificity, multiple infestation, and other ecological phenomena.

The observations discussed in this section were based in part on the results of the writer's examinations of seventy-one bullfrogs, sixty southern leopard-frogs, sixty-two Fowler's toads, sixty spadefoots, fifty-five chorus-frogs, and sixty spring peepers. The hosts were taken at fairly regular intervals throughout the year from March, 1934 to March, 1935 (Table 1). The species selected are of especial interest in that each is characteristic of a different habitat.

PARASITES AND HABITATS

The species of Salientia studied by the writer can be arranged in a series comprising various extents of preference for aquatic, terrestrial, and arboreal habitats. None of the frogs and toads studied have attained complete freedom from the water. Even the most completely terrestrial, the fossorial spadefoot, must visit an aquatic environment in order to spawn but may limit this visit to a single day annually. The other five species spend considerable time at the ponds and streams.

Table 2 shows that salientians at Washington, North Carolina, are almost always parasitized by protozoans, especially those that live in the intestine. Blood protozoans are more often found in the aquatic hosts. This observation agrees with the findings of Hegner (1929) who studied the protozoans in the aquatic and terrestrial phases of *Triturus viridescens* and suggests an inter-

mediary aquatic blood-sucking vector. Except for their unusual abundance in the hylids, intestinal ciliates appear to become more prevalent as more completely terrestrial host species are considered.

The most aquatic species, *Rana catesbeiana*, showed a greater infestation with metazoan parasites than did any other species Metazoan parasites (Table 14) were found in every individual of this host species except one which was very young. The average number of metazoan parasites was 133. The distinctly less aquatic southern leopard-frog contained metazoan parasites in every case but the average number was less (76.7). Fowler's toad, which spends but about one month annually in an aquatic environment, showed metazoan parasites in all cases but two. The average number of metazoan parasites was 23.9. The least aquatic species, the spadefoot, harbored metazoan parasites in 83.3 per cent of the sixty hosts examined. The average number of parasites per host was 18.9. The data from comparisons of frogs and toads of moderate size suggest a high correlation between an aquatic habitat preference and degree of metazoan parasitism.

Continuing the comparison to include the two small hylids studied, it is apparent that *Hyla crucifer* contained distinctly fewer metazoan parasites than did *Pseudacris brimleyi*. The former was infested to the extent of 65 per cent, average number per host 10.6; the latter was infested in 98.2 per cent of the individuals examined and harbored an average number of 14.7. These data suggest that an arboreal habitat is less conducive to metazoan parasitism than a more terrestrial habitat.

More trematode parasites occur in aquatic than in terrestrial species of hosts (Table 3). This finding is in agreement with those of Pearse (1932) in his study of the parasites of Japanese salamanders. The preponderance of lung flukes in the more aquatic hosts is understandable in light of the work done on the life-histories of these trematodes (Krull 1930, 1931, 1932, 1933, 1934; Ingles 1933), all of which require aquatic intermediate hosts in addition to snails. The prevalence of larval flukes is significantly correlated with residence of the host in an aquatic habitat. This correlation is in agreement with the known methods of entrance of cercariae and metacercariae both by direct penetration of the skin of the host and by ingestion with food of aquatic origin. The complete absence of flukes from the least aquatic species, the spadefoot, is noteworthy. This suggests that the assumption of a subterranean habitat with an almost complete reduction of the time spent in an aquatic habitat at the breeding season, has minimized effectively the continuance of trematode parasitism. In the Hylidae, it appears that the resumption of palustrine life, as illustrated by *Pseudacris brimleyi*, has increased the degree of trematode parasitism. *Hyla crucifer*, however, living in a less monotonous habitat than does *Pseudacris brimleyi*, contained a greater variety of parasite species.

A comparison of cestode parasites is presented in Table 4. Cestode infestation does not show the correlation with habitat so clearly indicated in the foregoing discussion. That habitat preference is an important factor is apparent but it is also clear that no single factor is sufficient in itself to explain all the observations. It is likewise apparent here that host specificity is of considerable importance especially in reference to adult cestodes. *Distoichometra bufonis* is known only from Bufo and Scaphiopus hosts. The similarity in adaptation of these hosts suggests the possibility of similarity in internal physiological conditions. The differently adjusted, more aquatic species do not harbor this common salientian cestode. It is worthy of note that the Bufo harbors significantly more of these cestodes than does Scaphiopus and this observation suggests that Distoichometra may resemble *Ophiotaenia saphena* in gaining entrance to its definitive host through ingested food of aquatic origin (Thomas 1931). The evidence presented herein does not suggest the direct development of Distoichometra, as has been found for the closely related Cylindrotaenia (Joyeux 1924).

Data concerning the variation of nematode parasites is presented in Table 5. It appears that a lower percentage of infestation by nematodes occurred in the arboreal spring-peeper than in the more terrestrial chorus-frog. This is especially noticeable in the prevalence of nematodes inhabiting lungs and intestine. Agamonema, however, was much more prevalent in the tree frog. Comparison of Scaphiopus, Bufo and Rana shows no significant regularity in nematode infestation in general. Pearse (1932) found that the nematodes of Japanese salamanders from different habitats were erratic in distribution. Considering the prevalence of encysted nematodes and nematodes of the intestine of hosts of the same three genera, the irregularity again is apparent. In the case of the filaroids, which were restricted to hosts of the genus Rana, a significant correlation appears and this suggests that these nematodes are in some manner connected with an aquatic blood-sucking vector. Rhabdias is prevalent only in the two palustrine species. This observation suggests that the free living stages of Rhabdias reach an optimum in a moist terrestrial habitat. The distribution of Oswaldocruzia suggests a similar adjustment to a considerably less moist terrestrial habitat. Intestinal oxyuroids tend to be more prevalent in more terrestrial hosts but the correlation is not as clear as in the other cases.

The prevalence of the larval acanthocephalan, Centrorhynchus (Table 6), appears sgnificantly correlated with the residence of the host in an aquatic environment. Since acanthocephalans are generally associated with a host in all stages of their life-histories, this suggests that infestation follows ingestion of an aquatic intermediate host.

The distribution of the larval mite, *Hannemania penetrans*, is erratic. Leeches were found only on the most aquatic species of host (Table 6).

SEASONAL VARIATIONS

The data presented in Tables 7-13 may be interpreted as indicating seasonal variations in some of the parasites of the Salientia studied. In many cases, however, the observed variations cannot be regarded as significantly related to seasonal changes. The attempt has been made to correlate the variations with the phases of activity of the hosts as well as the annual progression of the seasons.

The intestinal protozoa, whether considered specifically or as a group, show no marked seasonal variation. The occurrence of trypanosomes appears, however, to be correlated with the residence of the host in an aquatic environment. In hosts which are largely aquatic infestation with these flagellates was highest during the warmer months of the year. This may be due to an aquatic blood-sucking vector which feeds more actively in the warmer months of the year. This opinion is supported by the work of Franca (1908) who found that frog trypanosomes were transmitted by leeches in Europe. The haemosporidians, Karyolysus and Lankesterella, also reach a maximum in the warmer months. Miss Sanders' (1928) observations lead her to believe that Karyolysus in frogs is not transmitted by a leech but by a vector which attacks a frog but not a tadpole. Transmission of Lankesterella has been reported as being effected by the bites of leeches (Noller 1913a). It is also worthy of note that all three of the blood protozoans studied by the writer are quite generally absent from the less aquatic hosts.

Cytamoeba occurs but rarely in hosts other than *Rana sphenocephala* and reaches its maximum in November and minimum in May. It is possible that this variation represents an adaptation to the common winter breeding habit of this host. Noller (1913) thinks that a leech is probably the vector of this parasite. The variations shown by the unidentified protozoan cysts in the muscles of the bullfrog are erratic.

Trematodes of the genus Glypthelmins, which were found in the bullfrog and in the spring-peeper, failed to show significant correlations with seasonal variations. Lung flukes, however, appeared to bear out the contention of Ward (1909) that the parasites of *Rana pipiens* are lost at the time of spawning and that new infestations gradually increase to a maximum at the time of hibernation. Krull (1931) also has observed that frogs annually lose their lung flukes and take on fresh infestations.

The variations shown by bladder flukes appear to indicate that their prevalence is associated with the residence of the host in an aquatic habitat and with higher temperatures. The terrestrial toad harbored these flukes chiefly in the months following the breeding season. The bullfrog had a maximum infestation in midsummer and the southern leopard-frog was infested only at the time of breeding. Small bullfrogs were infested only in March and August.

The occurrence of Diplodiscus, while somewhat erratic, tends in the case of the large bullfrogs, to bear out the previously cited contention of Ward. The evidence, however, is by no means clear cut and is especially weak regarding the time of loss of the parasites. The appearance of this fluke in *Rana sphenocephala, Hyla crucifer* and *Pseudacris brimleyi* after these species have left the breeding places supports the belief that infestation follows ingestion of molted skin containing metacercariae. If these metacercariae accumulate on the skin during the breeding season, infestation would be expected following the first molt thereafter.

Brachycoelium occurred regularly only in the chorus-frog. The prevalence of this parasite appears to be correlated with the residence of the host in an aquatic environment. The life-history of the fluke is unknown but an aquatic secondary host probably is necessary.

When all marital flukes are considered it appears that the variation is quite erratic. Only the southern leopard-frog, which is closely related to *Rana pipiens*, shows variations which are in substantial agreement with the theories of Ward. The prevalence of larval flukes is generally erratic.

Adult cestodes reached a maximum shortly after the breeding season of each host species infested. The data suggest the agency of an aquatic intermediate host for both *Ophiotaenia saphena* and *Distoichometra bufonis*. Thomas (1931) has found that frogs become infested with *O. saphena* by ingesting copepods but the life-history of Distoichometra is unknown.

Encysted larval proteocephalids were very erratic but showed a tendency to become more abundant during the hosts residence in an aquatic environment, especially in those species which harbored few of these parasites.

The nematodes in general show erratic variation. Oswaldocruzia in the less aquatic hosts appeared to be more prevalent after the host had spent some time in an aquatic environment. The prevalence of Foleyella and Microfilaria showed minima at the time of breeding with maxima before the breeding seasons, thus being in agreement with Ward's theories.

Leeches were found only in midsummer and mites were erratic in their occurrence.

VARIATION OF PARASITES WITH SIZE AND AGE OF HOST

The data presented in the section on Parasites of Hosts Examined indicate important differences in infestation of large bullfrogs as compared with that of smaller and presumably younger individuals. The large *Rana catesbeiana* were infested with ten species of protozoans but only eight species were harbored by the individuals under 100 mm. in length. Each size group was infested by the same species of trematodes but these parasites were much more often found in the large individuals. The percentage of infestation and average number of parasites 100 per cent and 47.3 in the large bullfrogs

and 89.4 per cent and 10.42 in the small individuals. Adult cestodes were found only in the large hosts but larval cestodes occurred in both groups of bullfrogs. The percentage of infestation and average number of parasites of the latter type were 42.4 per cent and 32.5 in the large bullfrogs and 42.2 per cent and 3.58 in the small individuals. Nematodes were more common in large individuals (14 species, 100%, 166.0 average) than in small (8 species, 60.6%, 1.63 average). The larval acanthocephalan, Centrorhynchus, infested both large (78.8%, 12.6 average) and small (5.25%, 0.303 average) bullfrogs. Leeches were found attached to both large (12.1%, 0.303 average) and small (5.25%, 0.079 average) individuals. Hannemania (12.1%, 0.243 average) was restricted to large bullfrogs. Considering all metazoan parasites, the large *Rana catesbeiana* showed 100 per cent infestation and 259.2 average number of parasites per host while the small individuals were 97.4 per cent infested and harbored an average number of 15.8 parasites per host.

Host Specificity

The parasites found offer little or no evidence of a strict host specificity in the Salientia examined. Of the fifty-six species of parasites found only sixteen were restricted to a single host, i.e. *Glypthelmins* sp., *G. subtropica*, *Haematoloechus longiplexus*, *H. breviplexus*, *Ostiolum complexus*, *Gorgoderina translucida*, *G. simplex*, *Oswaldocruzia leidyi*, *Macrodella ditetra*, *Diplodiscus intermedius*, *Opalina kennicotti*, *Cephalogonimus americanus*, *Ophiotaenia saphena*, *Spironoura catesbeianae*, *Oxysomatium longicaudata*, and *Spiroxys* sp. were found associated with only one of the six species studied. All of these parasites with the likely exception of the probably undescribed *Glypthelmins* sp. and *Spiroxys* sp., have, however, been recorded from other hosts by a number of authors. It follows, then, that the parasites of the North Carolina Salientia studied show little or no host specificity.

Multiple Infestation

Multiple infestation is of common occurrence in the Salientia examined by the author. A few cases selected to show the extent of this phenomenon are presented in Table 15. This table shows that single individuals of *Scaphiopus holbrookii* and *Hyla crucifer* harbor as many as seven species of parasites. Two *Bufo fowleri* each contained eight species of parasites and one *Pseudacris brimleyi* contained seven. One individual of *Rana sphenocephala* and one of *R. catesbeiana* harbored thirteen and seventeen species of parasites respectively.

New Species, New Hosts

Three new species of parasites were found during the course of this study. These are a trematode of the genus Glypthelmins and two nematodes of the genera Spiroxys and Dujardinia. A fourth, a larval acanthocephalan of the

genus Centrorhynchus, is of uncertain status.   The new species will be described in a separate paper.   The genus Glypthelmins is known from a number of North American frogs but adult Spiroxys have been found in frogs only of Asiatic Rana.   Hedrick (1935) has reported the larvae of Spiroxys in American frogs.   Dujardinia has been reported from a toad, *Bufo marinus,* by Pearse (1936).

The following are the writer's new host records:

Scaphiopus holbrookii;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina carolinensis, O. triangulata, Distoichometra bufonis, Proteocephalid cysts, *Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia leidyi, O. pipiens, Physaloptera* sp., *Rhabdias ranae;*

Bufo fowleri;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina triangulata, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Gorgodera amplicava, Gorgoderina attenuata, G. simplex, G. translucida, Trematode cysts, *Distoichometra bufonis,* Proteocephalid cysts, *Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus, Hannemania penetrans;*

Pseudacris brimleyi;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina chorophili, O. hylaxena, O. oblanceolata, O. obtrigonoidea, O. pickeringii, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Diplodiscus temperatus, Trematode cysts, *Agamascaris odontocephala, Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus* sp.;

Hyla crucifer;

Nyctotherus cordiformis, Octomitus intestinalis, Opalina chorophili, O. hylaxena, O. virguloidea, Trichomonas augusta, Trypanosoma rotatorium, Brachycoelium hospitale, Diplodiscus temperatus, Glypthelmins, Trematode cysts, Proteocephalid cysts, *Agamascaris odontocephala, Agamonema* sp., *Cosmocercoides dukae, Oswaldocruzia pipiens, Physaloptera* sp., *Rhabdias ranae, Centrorhynchus* sp.;

Rana catesbeiana;

Entamoeba ranarum, Leptotheca ohlmacheri, Octomitus intestinalis, Loxogenes bicolor, Ophiotaenia saphena, Proteocephalid cysts, *Dujardinia* sp., *Oxysomatium longicaudata, Physaloptera* sp., *Spiroxys* sp., *Centrorhynchus* sp., *Macrobdella ditetra, Hannemania penetrans;*

Rana sphenocephala;

Cytamoeba bacterifera, Entamoeba ranarum, Karyolysus sp., *Lankesterella* sp., *Leptotheca ohlmacheri, Nyctotherus cordiformis, Octomitus intestinalis,*

Opalina kennicotti, O. obtrigonoidca, Trichomonas augusta, Cephalogonimus americanus, Gorgoderina attenuata, Loxogenes bicolor, Ostiolum complexus, Trematode cysts, Proteocephalid cysts, *Agamascaris odontocephala, Agamonema* sp., *Dujardinia* sp., *Foleyella americana, F. ranae, Microfilaria* sp., *Centrorhynchus* sp., *Hannemania penetrans.*

SUMMARY

1. Periodic examinations on 71 bullfrogs, 60 southern leopard-frogs, 62 Fowler's toads, 60 spadefoots, 55 chorus-frogs, and 60 spring-peepers were made during the course of a year.

2. Salientians habitually residing in aquatic habitats were more often parasitized with blood protozoans, trematodes, acanthocephalans and leeches.

3. Seasonal periodicity was observed only in relatively few of the parasites found.

4. Larger, and presumably older, bullfrogs harbored considerably greater numbers of parasites than smaller individuals.

5. Few of the parasites observed occur in a single host.

6. Multiple infestations are common in the salientians studied. As many as seventeen species of parasites were found in a single bullfrog.

7. The total number of parasite species distinguished in each of the six salientian hosts studied were: *Rana catesbeiana*, 35; *Rana sphenocephala*, 30; *Bufo fowleri*, 22; *Scaphiopus holbrookii*, 15; *Pseudacris brimleyi*, 20; and *Hyla crucifer*, 21.

TABLE 1. Showing seasonal distribution of salientians examined for parasites, 1934-1935. Figures show number of hosts examined.

Species	January	February	March	April	May	June	July	August	September	October	November	December	Total
Rana catesbeiana over 100 mm.	0	4	1	4	2	5	3	1	1	0	2	10	33
Rana catesbeiana under 100 mm.	10	0	4	1	3	0	2	4	4	5	5	0	38
Rana catesbeiana all sizes	10	4	5	5	5	5	5	5	5	5	7	10	71
Rana sphenocephala	5	5	5	5	5	5	5	5	5	5	5	5	60
Bufo fowleri	15	4	5	5	5	5	5	5	5	5	2	1	62
Scaphiopus holbrookii	11	4	5	5	5	5	5	5	5	5	5	0	60
Pseudacris brimleyi	8	3	5	5	5	1	3	5	0	10	7	3	55
Hyla crucifer	9	5	5	5	5	1	5	5	0	2	8	10	60

TABLE 2. Protozoan Parasites of Salientians. Figures indicate percentage of hosts infested.

Host	Blood Protozoa	Trypanosome	Karyolysus & Lankesterella	Cytamoeba	Intestinal Protozoa	Intestinal Ciliates	Intestinal Flagellates
Rana catesbeiana over 100 mm.	33.3	9.13	24.2	6.06	96.8	9.09	96.8
Rana catesbeiana under 100 mm.	13.2	10.5	5.25	0.0	100.0	0.0	100.0
Rana sphenocephala	71.7	38.3	28.3	40.0	96.7	38.3	93.3
Bufo fowleri	3.21	3.21	0.0	0.0	96.8	51.7	96.8
Scaphiopus holbrookii	0.0	0.0	0.0	0.0	94.5	65.1	83.7
Pseudacris brimleyi	1.8	1.8	0.0	0.0	92.7	83.7	65.5
Hyla crucifer	5.0	5.0	0.0	0.0	98.3	86.7	86.7

TABLE 3. Trematode Parasites of Salientians. The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Host	Lung Flukes	Intestinal Flukes	Bladder Flukes	All Marital Flukes	Larval Flukes	All Flukes
Rana catesbeiana over 100 mm.	60.7 2.09	94.0 12.2	72.7 10.0	100.0 24.2	69.7 23.1	100.0 47.3
Rana catesbeiana under 100 mm.	18.4 0.42	73.7 3.13	7.91 0.158	84.3 3.7	63.2 6.72	89.4 10.42
Rana sphenocephala	56.7 5.72	45.0 1.11	5.0 0.083	56.7 7.0	53.3 37.8	88.3 44.8
Bufo fowleri	0.0 0.0	1.61 0.016	8.07 0.129	8.07 0.145	21.0 0.58	29.1 0.726
Pseudacris brimleyi	0.0 0.0	76.4 6.74	0.0 0.0	76.4 6.74	3.6 2.38	76.4 9.13
Hyla crucifer	0.0 0.0	26.7 2.02	0.0 0.0	26.7 2.02	3.33 0.033	30.0 2.05

Table 4. Cestode Parasites of Salientians.* The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Hosts	Adult Cestodes	Larval Cestodes	All Cestodes
Rana catesbeiana, over 100 mm.	9.09 0.091	42.4 32.5	48.5 32.6
Rana catesbeiana, under 100 mm.	0.0 0.0	42.2 3.58	42.2 3.58
Rana sphenocephala	0.0 0.0	51.7 10.0	51.7 10.0
Bufo fowleri	40.3 1.97	3.21 1.61	43.6 3.58
Scaphiopus holbrookii	16.7 0.92	1.7 0.33	18.3 1.25
Hyla crucifer	0.0 0.0	3.33 0.134	3.33 0.134

* *Pseudacris brimleyi* harbored no cestodes.

Table 5. Nematode Parasites of Salientians. The upper figures indicate percentage of hosts infested and the lower figures average number of parasites per individual.

Host	Intestinal Nematodes	Lung Nematodes	Encysted Nematodes	Intestinal Oxyuroids	Intestinal Strongyloids	Filaroids	All Nematodes
Rana catesbeiana over 100 mm.	81.8 33.3	12.1 0.182	96.9 132.4	81.8 33.15	9.1 0.053	54.6 3.7	100.0 166.0
Rana catesbeiana under 100 mm.	21.1 0.395	15.8 0.237	23.7 0.527	5.25 0.053	18.4 0.342	2.63 0.0263	60.6 1.63
Rana sphenocephala	48.3 2.26	48.3 2.48	76.7 5.77	3.33 0.083	48.3 2.18	33.3 1.03	95.0 19.3
Bufo fowleri	72.6 4.0	1.61 0.048	42.5 15.8	32.3 0.5	61.3 3.5	0.0 0.0	91.8 19.5
Scaphiopus holbrookii	75.0 11.8	1.7 0.017	26.7 5.62	71.7 10.0	43.3 1.75	0.0 0.0	83.3 17.6
Pseudacris brimleyi	87.3 3.78	41.8 0.8	10.9 0.49	80.0 2.66	40.0 1.05	0.0 0.0	91.0 5.47
Hyla crucifer	18.4 0.784	3.33 0.083	25.0 7.5	16.7 0.234	8.33 0.55	0.0 0.0	41.7 8.4

TABLE 6. Acanthocephala, Hirudinea, and Acarina.* Upper figures indicate percentage of hosts infested and the lower figures the average number of parasites per individual.

Host	Centrorhynchus	Macrobdella	Hannemania
Rana catesbeiana, over 100 mm.	78.8 12.6	12.1 0.303	12.1 0.243
Rana catesbeiana, under 100 mm.	5.25 0.132	5.25 0.079	0.0 0.0
Rana sphenocephala	28.3 2.62	0.0 0.0	6.67 0.1
Bufo fowleri	1.61 0.0161	0.0 0.0	4.83 0.145
Pseudacris brimleyi	7.3 0.127	0.0 0.0	0.0 0.0
Hyla crucifer	1.67 0.0167	0.0 0.0	0.0 0.0

' None of these parasites were harbored by *Scaphiopus holbrookii*.

TABLE 7. Seasonal Variation of Parasites. *Rana catesbeiana* (over 100 mm.). The first figures indicate percentage of infestation, the second, when given, indicate average number of parasites per individual.

Phase	Pre-breeding	Breeding	Post-breeding	Autumn	Hibernating
Average Date	Feb. 10	April 28	July 6	Oct. 10	Dec. 16
Range of Dates	Feb. 10	Mar.28-June 6	June28-July22	Aug.29 -Nov.9	Dec. 16
No. Exam	4	8	7	4	10
Aver. Length mm.	139.5	139.2	127.1	134.1	160.2
Cytamoeba	25.0	0.0	0.0	0.0	10.0
Entamoeba	0.0	12.5	0.0	0.0	0.0
Protozoan cysts in muscles	25.0	37.5	14.3	75.0	60.0
Karyolysus or Lankesterella	0.0	25.0	28.6	25.0	30.0
Leptotheca	0.0	0.0	0.0	25.0	0.0
Nyctotherus	25.0	12.5	0.0	25.0	0.0
Octomitus	100.0	62.5	85.7	100.0	90.0
Trichomonas	100.0	100.0	100.0	75.0	100.0
Trypanosoma	0.0	12.5	28.6	0.0	0.0
All Intestinal Flagellates	100.0	100.0	100.0	100.0	100.0
All Intestinal Protozoa	100.0	100.0	100.0	100.0	100.0
All Blood Protozoa	25.0	25.0	57.2	25.0	30.0
All Protozoa	100.0	100.0	100.0	100.0	100.0
Diplodiscus	75.0 4.25	25.0 2.75	85.7 2.85	75.0 15.0	100.0 12.1
Bladder Flukes	25.0 0.25	87.5 11.13	100.0 21.7	75.0 14.5	60.0 3.7
Glypthelmins	50.0 5.0	62.5 2.75	28.6 0.428	0.0 0.0	90.0 8.8
Haematoloechus	75.0 2.75	25.0 0.25	71.4 1.29	75.0 6.25	70.0 2.2
Loxogenes	0.0 0.0	37.5 2.37	28.6 2.14	50.0 1.75	50.0 0.8

TABLE 7, continued.

Phase	Pre-breeding	Breeding	Post-breeding	Autumn	Hibernating
Average Date	Feb. 10	April 28	July 6	Oct. 10	Dec. 16
Range of Dates	Feb. 10	Mar.28-June 6	June28-July22	Aug.29 -Nov.9	Dec. 16
No. Exam	4	8	7	4	10
Aver. Length mm.	139.5	139.2	127.1	134.1	160.2
Encysted Flukes	75.0	62.5	71.4	, 50.0	100.0
	14.5	37.5	14.9	12.3	31.6
All Marital Flukes	100.0	100.0	100.0	100.0	100.0
	12.25	19.25	28.41	37.5	27.6
All Flukes	100.0	100.0	100.0	100.0	100.0
	26.75	56.75	43.31	49.8	59.2
Ophiotaenia	0.0	25.0	14.3	0.0	0.0
	0.0	0.25	0.143	0.0	0.0
Proteocephalid	25.0	25.0	0.0	50.0	90.0
Cysts	1.0	26.25	0.0	95.8	47.6
All Cestodes	25.0	37.5	14.3	50.0	90.0
	1.0	26.5	0.143	95.8	47.6
Agamascaris	0.0	12.5	57.2	50.0	70.0
	0.0	0.125	0.714	1.5	1.1
Agamonema	100.0	87.5	85.7	75.0	100.0
	78.25	44.8	35.9	180.5	254.6
Cosmocercoides	0.0	62.5	0.0	25.0	0.0
	0.0	5.37	0.0	0.5	0.0
Dujardinia	50.0	25.0	0.0	0.0	30.0
	3.0	0.375	0.0	0.0	1.0
Foleyella	25.0	50.0	14.3	75.0	90.0
	1.0	4.5	0.286	5.25	6.1
Oswaldocruzia	0.0	25.0	0.0	25.0	0.0
	0.0	0.375	0.0	0.25	0.0
Oxysomatium	75.0	37.5	28.6	0.0	0.0
	6.25	17.5	5.57	0.0	0.0
Physaloptera	0.0	25.0	71.4	50.0	50.0
	0.0	0.5	3.0	1.0	2.7
Rhabdias in lungs	0.0	12.5	14.3	50.0	0.0
	0.0	0.125	0.286	0.75	0.0
Rhabdias in body	0.0	0.0	0.0	25.0	0.0
cavity	0.0	0.0	0.0	0.5	0.0
Spironoura	0.0	50.0	42.8	50.0	60.0
	0.0	63.62	29.71	41.0	4.2
Spiroxys	0.0	12.5	28.6	0.0	0.0
	0.0	0.25	3.0	0.0	0.0
All Nematodes in	100.0	87.5	85.7	100.0	100.0
Definitive Host	7.25	92.24	41.85	49.25	13.0
All Encysted	100.0	100.0	100.0	75.0	100.0
Nematodes	81.25	45.3	36.6	182.0	256.7
All Nematodes	100.0	100.0	100.0	100.0	100.0
	88.5	137.5	78.45	231.3	269.7
Centrorhynchus	75.0	87.5	57.2	75.0	100.0
	3.75	22.0	8.86	10.0	16.5
Macrobdella	0.0	0.0	57.2	0.0	0.0
	0.0	0.0	1.43	0.0	0.0
Hannemania	0.0	0.0	42.8	25.0	0.0
	0.0	0.0	0.714	0.75	0.0
All Metazoans	` 100.0	100.0	100.0	100.0	100.0
	112.3	209.9	132.9	387.7	393.9

TABLE 8. Seasonal Variation of Parasites. *Rana catesbeiana* (under 100 mm.). The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase	Midwinter	Spring	Early Summer	Late Summer	Autumn
Average Date	Jan. 10	Mar. 22	May 25	Aug. 22	Oct. 28
Range of Dates	Jan. 10	Mar. 4-Apr. 27	May22-May28	Jul.22-Sept. 30	Oct.11–Nov.29
No. Exam	10	5	3	10	10
Aver. Length mm.	36.0	49.0	64.9	48.9	41.8
Entamoeba	30.0	0.0	33.3	0.0	10.0
Karyolysus or					
Lankesterella	0.0	0.0	33.3	10.0	0.0
Leptotheca	70.0	0.0	0.0	10.0	50.0
Octomitus	90.0	100.0	100.0	100.0	100.0
Trichomonas	70.0	80.0	100.0	90.0	50.0
Trypanosoma	0.0	0.0	33.3	20.0	10.0
Unidentified					
Flagellates	0.0	40.0	33.3	20.0	10.0
All Blood Protozoa	0.0	0.0	33.3	30.0	10.0
All Intestinal					
Flagellates	100.0	100.0	100.0	100.0	100.0
All Protozoa	100.0	100.0	100.0	100.0	100.0
Bladder Flukes	0.0	20.0	0.0	20.0	0.0
	0.0	0.2	0.0	0.5	0.0
Diplodiscus	70.0	0.0	100.0	30.0	50.0
	1.4	0.0	4.0	3.4	1.2
Glypthelmins	0.0	20.0	0.0	0.0	0.0
	0.0	3.0	0.0	0.0	0.0
Haematoloechus	10.0	40.0	0.0	20.0	20.0
	0.1	0.4	0.0	0.6	0.7
Loxogenes	40.0	40.0	100.0	30.0	60.0
	0.7	0.6	2.33	0.8	1.1
All Marital Flukes	80.0	80.0	100.0	80.0	90.0
	2.2	4.2	6.33	5.3	3.0
Encysted Flukes	50.0	80.0	100.0	40.0	80.0
	7.8	23.0	17.0	3.1	1.9
All Flukes	80.0	100.0	100.0	80.0	100.0
	6.1	27.2	23.3	8.2	4.7
Proteocephalid	50.0	40.0	33.3	50.0	30.0
Cysts	2.6	8.6	7.33	4.0	0.5
Agamascaris	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Agamonema	20.0	20.0	33.3	30.0	0.0
	0.2	0.4	3.0	0.5	0.0
Cosmocercoides	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Foleyella	0.0	20.0	0.0	0.0	0.0
	0.0	0.2	0.0	0.0	0.0
Oswaldocruzia	10.0	60.0	0.0	10.0	20.0
	0.2	1.4	0.0	0.2	0.2
Rhabdias in lungs	0.0	20.0	0.0	40.0	10.0
	0.0	0.2	0.0	0.7	0.1
Rhabdias in body	30.0	0.0	0.0	20.0	30.0
Cavity	0.3	0.0	0.0	0.7	0.8
Spironoura	0.0	0.0	0.0	10.0	0.0
	0.0	0.0	0.0	0.1	0.0
All Nematodes in	40.0	80.0	0.0	60.0	60.0
Definitive Host	0.5	2.0	0.0	1.7	1.1
All Encysted	20.0	40.0	33.3	30.0	0.0
Nematodes	0.2	0.6	3.0	0.5	0.0
All Nematodes	40.0	100.0	33.3	70.0	60.0
	0.7	2.6	3.0	2.2	1.1
Centrorhynchus	0.0	20.0	0.0	10.0	0.0
	0.0	0.2	0.0	0.4	0.0
Macrobdella	0.0	0.0	0.0	20.0	0.0
	0.0	0.0	0.0	0.3	0.0
All Metazoans	90.0	100.0	100.0	100.0	100.0
	9.4	38.6	33.7	15.1	6.3

TABLE 9. Seasonal Variation of Parasites. *Rana sphenocephala*. The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase	Breeding	Post-breeding	Midsummer	Early Winter
Average Date	Feb. 9	May 14	Aug. 15	Nov. 12
Range of Dates	Jan. 10-Mar. 4	Apr. 18-June 6	July 6-Sept. 9	Oct. 11-Dec. 21
No. Exam.	15	15	15	15
Average Length mm	55.9	55.1	53.4	56.0
Cytamoeba	53.3	6.67	40.0	60.0
Entamoeba	6.67	0.0	0.0	0.0
Karyolysus or Lankesterella	20.0	26.7	40.0	26.7
Leptotheca	20.0	0.0	0.0	20.0
Nyctotherus	6.67	13.3	20.0	13.3
Octomitus	100.0	93.3	80.0	93.3
Opalina	40.0	46.7	20.0	13.3
Trichomonas	86.7	80.0	86.7	60.0
Trypanosoma	13.3	46.7	53.3	40.0
All Ciliates	40.0	53.3	26.6	26.6
All Intestinal Flagellates	100.0	93.3	86.7	93.3
All Intestinal Protozoa	100.0	100.0	93.3	96.7
All Blood Protozoa	66.7	66.7	80.0	73.3
All Protozoa	100.0	100.0	93.3	96.7
Brachycoelium	6.67	6.67	0.0	0.0
	0.067	0.8	0.0	0.0
Cephalogonimus	6.67	0.0	0.0	0.0
	0.067	0.0	0.0	0.0
Diplodiscus	26.7	20.0	60.0	53.3
	1.13	0.867	0.8	0.667
Gorgoderina	13.3	6.67	0.0	0.0
	0.2	0.133	0.0	0.0
Loxogenes	0.0	6.67	6.67	6.67
	0.0	0.267	0.067	0.067
Ostiolum	33.3	66.7	66.7	66.7
	1.73	3.53	3.07	14.53
Encysted Flukes	33.3	46.7	66.7	66.7
	38.9	53.3	40.2	18.5
All Flukes in Definitive Host	60.0	66.7	80.0	86.7
	3.2	5.6	3.93	15.27
All Flukes	66.7	100.0	93.3	93.3
	42.1	58.9	44.13	33.77
Proteocephalid Cysts	40.0	53.3	76.7	40.0
	11.8	10.5	9.73	8.07
Agamascaris	26.7	6.67	6.67	33.3
	1.33	0.067	0.067	0.467
Agamonema	53.3	46.7	60.0	93.3
	4.33	2.6	1.4	8.27
Cosmocercoides	13.3	0.0	0.0	0.0
	0.33	0.0	0.0	0.0
Dujardinia	6.67	6.67	6.67	0.0
	0.067	0.267	0.133	0.0
Foleyella	26.7	26.7	33.3	46.7
	0.533	0.333	1.13	2.13
Microfilaria	0.0	6.67	6.67	13.3
Oswaldocruzia	66.7	40.0	33.3	53.3
	3.4	2.8	0.533	2.0
Rhabdias in lungs	60.0	33.3	46.7	53.3
	4.73	2.03	1.73	1.4
Rhabdias in body cavity	80.0	46.7	26.7	80.0
	19.1	0.867	0.333	14.7
All Intestinal Nematodes	66.7	40.0	33.3	53.3
	3.73	2.8	0.533	2.0
All Nematodes in Definitive Host	93.3	86.7	73.3	93.3
	28.13	6.07	3.73	20.23
All Encysted Nematodes	60.0	60.0	60.0	93.3
	5.73	2.93	1.6	8.74
All Nematodes	100.0	93.3	86.7	100.0
	33.86	9.0	5.33	28.97
Centrorhynchus	40.0	26.7	20.0	26.7
	1.67	7.34	0.533	0.867
Hannemania	6.67	13.3	0.0	6.67
	0.0133	0.2	0.0	0.067
All Metazoans	100.0	100.0	100.0	100.0
	89.44	85.97	59.72	71.75

TABLE 10.   Seasonal Variation of Parasites.   *Bufo fowleri.*   The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Phase..................	Hibernation	Emergence and Breeding	Midsummer	Pre-hibernation
Average Date..........	Jan. 15	May 1	Aug. 2	Oct. 24
Range of Dates........	Dec. 29-Feb. 14	Mar. 28-June 7	July 6-Sept. 7	Oct. 10-Nov. 23
No. Exam.............	20	20	15	7
Average Length mm. ...	48.9	48.9	47.1	48.3
Nyctotherus...........	30.0	25.0	53.3	42.8
Octomitus.............	60.0	60.0	40.0	42.8
Opalina...............	25.0	20.0	26.7	71.4
Trichomonas...........	90.0	95.0	93.3	100.0
Trypanosoma..........	0.0	0.0	13.3	0.0
All Ciliates...........	45.0	35.0	66.7	85.6
All Intestinal Flagellates.	95.0	100.0	93.3	100.0
All Intestinal Protozoa .	95.0	100.0	93.3	100.0
All Protozoa	95.0	100.0	93.3	100.0
Bladder Flukes........	5.0	5.0	13.3	14.3
	0.1	0.1	0.2	0.143
Brachycoelium..	0.0	0.0	0.0	14.3
	0.0	0.0	0.0	0.143
All Marital Flukes.	5.0	5.0	13.3	14.3
	0.1	0.1	0.2	0.286
Encysted Flukes.......	10.0	35.0	13.3	28.6
	0.6	0.5	0.6	0.714
All Flukes.............	15.0	40.0	26.7	42.8
	0.7	0.6	0.8	1.0
Distoichometra........	30.0	40.0	53.3	42.8
	1.2	2.1	3.33	0.856
Proteocephalid Cysts...	0.0	0.0	13.3	0.0
	0.0	0.0	6.67	0.0
All Cestodes..........	30.0	40.0	66.7	42.8
	1.2	2.1	10.0	0.856
Agamonema......	55.0	45.0	26.7	57.2
	34.0	3.95	12.75	4.14
Cosmocercoides........	15.0	45.0	40.0	14.3
	0.15	0.8	0.6	0.286
Oswaldocruzia........	35.0	65.0	86.7	71.4
	0.8	3.85	2.8	7.86
Physaloptera..........	0.0	0.0	6.67	0.0
	0.0	0.0	0.067	0.0
Rhabdias in lungs......	0.0	0.0	0.0	14.3
	0.0	0.0	0.0	0.428
Rhabdias in body cavity.	0.0	5.0	0.0	0.0
	0.0	0.1	0.0	0.0
All Intestinal Nematodes..........	45.0	80.0	100.0	71.4
	0.95	4.65	3.47	8.15
All Nematodes in Definitive Host	45.0	80.0	100.0	71.4
	0.95	4.75	3.47	8.56
All Nematodes.........	75.0	100.0	100.0	100.0
	34.95	8.7	16.2	12.7
Centrorhynchus........	0.0	0.0	6.67	0.0
	0.0	0.0	0.067	0.0
Hannemania..........	0.0	5.0	13.3	0.0
	0.0	0.05	0.533	0.0
All Metazoans........	90.0	100.0	100.0	100.0
	36.85	11.45	27.6	14.6

TABLE 11. Seasonal Variation of Parasites. *Scaphiopus holbrookii.* The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase............	Hibernating	Breeding	Early Summer	Late Summer	Autumn
Average Date....	Jan. 9	Mar. 16	May 30	Aug. 7	Oct. 10
Range of Dates...	Jan. 3-Jan. 10	Feb.25-Apr. 12	May15-June 6	July20 -Aug.26	Sept.16-Nov.4
No. Exam........	11	14	10	10	15
Aver. Length mm.	43.7	55.5	53.7	44.9	54.6
Nyctotherus......	54.5	50.0	60.0	50.0	73.4
Octomitus.......	81.7	42.8	50.0	80.0	66.7
Opalina..........	36.4	21.4	10.0	30.0	40.0
Trichomonas.....	91.0	57.2	80.0	80.0	80.0
All Ciliates	72.7	57.2	60.0	50.0	80.0
All Flagellates....	100.0	64.3	90.0	80.0	86.7
All Protozoa.....	100.0	85.7	100.0	80.0	100.0
Distoichometra...	9.1	28.6	20.0	0.0	20.0
	0.46	1.78	1.7	0.0	0.53
Proteocephalid					
Cysts.........	0.0	0.0	10.0	0.0	0.0
	0.0	0.0	2.0	0.0	0.0
All Cestodes......	9.1	28.6	30.0	0.0	20.0
	0.46	1.78	3.7	0.0	0.53
Agamonema......	9.1	14.3	40.0	30.0	40.0
	0.09	0.71	3.1	27.8	1.13
Cosmocercoides ..	72.7	78.6	70.0	70.0	66.7
	3.37	15.85	3.5	19.6	7.34
Oswaldocruzia....	27.3	64.3	60.0	50.0	20.0
	0.46	1.57	2.8	3.6	0.93
Physaloptera.....	0.0	0.0	0.0	0.0	13.3
	0.0	0.0	0.0	0.0	0.8
Rhabdias in lungs	9.1	0.0	0.0	0.0	0.0
	0.09	0.0	0.0	0.0	0.0
Rhabdias in body					
cavity.........	9.1	0.0	0.0	0.0	0.0
	0.09	0.0	0.0	0.0	0.0
All Intestinal	72.7	85.7	70.0	80.0	66.7
Nematodes.....	3.83	17.42	6.3	23.2	9.07
All Nematodes in	72.7	85.7	70.0	80.0	66.7
Definitive Host.	4.0	17.42	6.3	23.2	9.07
All Nematodes ...	72.7	85.7	90.0	90.0	80.0
	4.09	18.1	9.4	51.0	10.2
All Metazoans....	72.7	85.7	90.0	90.0	80.0
	4.54	19.9	13.1	51.0	10.72

TABLE 12. Seasonal Variation of Parasites. *Pseudacris brimleyi.* The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase	Pre-breeding	Breeding	Early Summer	Late Summer	Early Winter
Average Date	Jan. 11	Mar. 17	May 21	Aug. 12	Oct. 30
Range of Dates	Dec.31 -Jan.20	Feb.13 -Apr.17	Apr. 27-June 7	Jul.20 -Aug.26	Oct.10-Nov.29
No. Exam	11	12	7	8	17
Aver. Length mm.	27.5	28.6	27.8	24.7	27.8
Nyctotherus	63.7	16.7	0.0	50.0	23.6
Octomitus	63.7	33.3	85.7	62.5	53.0
Opalina	63.7	83.4	85.7	82.5	82.4
Trichomonas	9.1	50.0	28.6	37.5	29.4
Trypanosoma	0.0	0.0	0.0	0.0	5.9
All Ciliates	81.8	83.4	85.7	82.5	82.4
All Intestinal Flagellates	72.7	50.0	85.7	75.0	58.8
All Intestinal Protozoa	100.0	100.0	85.7	82.5	88.3
All Protozoa	100.0	100.0	85.7	82.5	88.3
Brachycoelium	81.8	83.4	71.4	50.0	70.6
	6.27	14.16	5.0	3.25	4.06
Diplodiscus	0.0	8.3	14.3	12.5	0.0
	0.0	0.083	0.143	0.125	0.0
All Marital Flukes	81.8	91.7	71.4	62.5	70.6
	6.27	14.25	5.14	3.38	4.06
Encysted Flukes	9.1	0.0	14.3	0.0	0.0
	0.09	0.0	18.6	0.0	0.0
Agamascaris	0.0	8.3	0.0	0.0	0.0
	0.0	0.083	0.0	0.0	0.0
Agamonema	27.3	8.3	0.0	0.0	5.9
	2.18	0.083	0.0	0.0	0.059
Cosmocercoides	90.9	91.7	85.7	62.5	64.7
	5.45	2.92	2.43	1.25	1.35
Oswaldocruzia	90.0	33.3	28.6	12.5	29.4
	1.45	0.58	3.15	0.125	0.71
Physaloptera	9.1	0.0	0.0	0.0	5.9
	0.45	0.0	0.0	0.0	0.059
Rhabdias in lungs	54.5	58.3	42.9	12.5	35.3
	1.09	1.67	0.43	0.125	0.47
Rhabdias in body cavity	18.2	16.7	14.3	0.0	29.4
	0.45	0.33	0.29	0.0	0.6
All Intestinal Nematodes	100.0	91.7	100.0	75.0	76.5
	7.35	3.5	5.58	1.38	2.12
All Nematodes in Definitive Host	100.0	100.0	100.0	75.0	82.4
	8.91	5.5	6.28	1.5	3.18
All Encysted Nematodes	100.0	16.7	0.0	0.0	5.9
	2.2	0.17	0.0	0.0	0.06
All Nematodes	100.0	100.0	100.0	75.0	82.4
	11.1	5.66	6.28	1.5	3.24
Centrorhynchus	0.0	8.3	0.0	0.0	17.7
	0.0	0.083	0.0	0.0	0.35
All Metazoans	100.0	100.0	100.0	87.5	100.0
	17.4	20.0	30.0	4.88	7.65

TABLE 13. Seasonal Variation of Parasites. *Hyla crucifer.* The upper figure indicates percentage of infestation, the lower, when given, indicates average number of parasites per individual.

Phase	Pre-breeding	Breeding	Post-breeding	Midsummer	Early Winter
Average Date	Dec. 30	Feb. 8	May 10	July 31	Nov. 14
Range of Dates	Dec. 27-31	Jan. 1-Mar. 4	Apr. 17-June 7	Jul. 9-Aug. 26	Oct.10–Nov.29
No. Exam	10	19	11	10	10
Aver. Length mm	27.8	28.6	26.5	20.8	26.4
Nyctotherus	60.0	47.3	36.4	30.0	40.0
Octomitus	90.0	68.4	45.5	80.0	50.0
Opalina	90.0	100.0	91.0	70.0	70.0
Trichomonas	90.0	52.6	72.8	40.0	80.0
Trypanosoma	10.0	5.26	9.1	0.0	0.0
All Ciliates	90.0	100.0	91.0	70.0	70.0
All Intestinal Flagellates	100.0	79.0	91.0	90.0	80.0
All Intestinal Protozoa	100.0	100.0	100.0	90.0	100.0
All Protozoa	100.0	100.0	100.0	90.0	100.0
Brachycoelium	0.0	10.5	18.2	0.0	0.0
	0.0	0.32	0.36	0.0	0.0
Diplodiscus	0.0	0.0	0.0	10.0	10.0
	0.0	0.0	0.0	0.1	0.1
Glypthelmins	20.0	10.5	18.2	10.0	40.0
	2.9	0.37	0.73	0.2	6.3
All Marital Flukes	20.0	21.0	36.4	20.0	40.0
	2.9	6.8	1.1	0.3	6.4
Encysted Flukes	0.0	5.26	9.1	0.0	0.0
	0.0	0.053	0.09	0.0	0.0
All Flukes	20.0	26.3	45.5	20.0	40.0
	2.9	0.74	1.18	0.3	6.4
Proteocephalid Cysts	0.0	10.5	0.0	0.0	0.0
	0.0	0.421	0.0	0.0	0.0
Agamascaris	0.0	0.0	0.0	0.0	10.0
	0.0	0.0	0.0	0.0	0.1
Agamonema	20.0	31.6	27.3	20.0	20.0
	0.3	4.79	16.6	1.9	15.4
Cosmocercoides	10.0	10.5	9.1	30.0	10.0
	0.2	0.105	0.091	0.4	0.1
Oswaldocruzia	10.0	5.26	0.0	0.0	30.0
	0.2	0.105	0.0	0.0	2.9
Physaloptera	10.0	0.0	9.1	0.0	0.0
	0.1	0.0	0.273	0.0	0.0
Rhabdias in lungs	0.0	5.26	9.1	0.0	0.0
	0.0	0.21	0.91	0.0	0.0
Rhadias in body cavity	0.0	5.26	0.0	0.0	0.0
	0.0	0.16	0.0	0.0	0.0
All Intestinal Nematodes	20.0	15.8	18.2	20.0	30.0
	0.5	0.21	0.36	0.4	3.0
All Encysted Nematodes	20.0	31.6	27.3	20.0	30.0
	0.3	4.8	16.6	1.9	15.5
All Nematodes	40.0	42.2	36.4	50.0	40.0
	0.8	5.37	16.9	2.4	18.4
Centrorhynchus	10.0	0.0	0.0	0.0	0.0
	0.1	0.0	0.0	0.0	0.0
All Metazoans	50.0	68.4	63.6	60.0	80.0
	3.8	6.53	18.1	2.7	24.8

TABLE 14. Comparison of Parasites in Hosts of Different Habitat Preference, 1934-1935. The first figure indicates percentage of infestation, the second, when given, indicates average number of parasites per individual.

Host	Number Examined	Average Length	Blood Protozoa	Intestinal Protozoa	Trematodi	Cestoda	Nematoda	Acantho-cephala	Metazoan Parasites
Scaphiopus holbrookii	60	51.0	0.0	94.5	0.0 0.0	18.3 1.25	83.3 17.6	0.0 0.0	83.3 18.9
Bufo fowleri	62	48.5	3.21	96.8	29.1 0.73	43.6 3.58	91.8 19.6	1.61 0.016	96.8 23.9
Rana sphenocephala	60	55.1	71.7	96.7	88.3 44.8	51.7 10.0	95.0 19.3	28.3 2.62	100.0 76.9
Rana catesbeiana (large)	33	143.2	33.3	96.8	100.0 47.3	48.5 32.6	100.0 166.0	78.8 12.6	100.0 259.2
Rana catesbeiana (small)	38	44.9	13.2	100.0	89.4 10.42	42.2 3.58	60.6 1.63	5.25 0.132	97.4 15.8
Rana catesbeiana (all sizes)	71	90.2	22.5	98.6	94.3 27.6	45.1 17.1	78.9 77.9	39.4 5.93	98.6 128.9
Pseudacris brimleyi	55	27.4	1.8	92.7	76.4 9.13	0.0 0.0	91.0 5.47	7.3 0.127	95.2 14.7
Hyla crucifer	60	26.4	5.0	98.3	30.0 2.05	3.33 0.134	41.7 8.4	1.67 0.017	65.0 10.6

TABLE 15. Multiple Infestation. The figures indicate the greatest number of parasite species observed in a single individual.

Host	Protozoa	Trematoda	Cestoda	Nematoda	Acantho-cephala	Annelida	Arthropoda	All Parasites
Scaphiopus holbrookii	4	0	1	4	0	0	0	7
Hyla crucifer	5	2	1	4	1	0	0	7
Bufo fowleri	5	3	1	3	1	0	1	8
Pseudacris brimleyi	4	3	0	5	1	0	0	9
Rana sphenocephala	6	5	1	5	1	0	1	13
Rana catesbeiana	5	8	2	8	1	1	1	17

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THE EFFECT OF RAINFALL AND TEMPERATURE ON THE ANNUAL RADIAL GROWTH OF PINE IN THE SOUTHERN UNITED STATES

By

T. S. COILE

Duke Forest, Duke University
Durham, N. C.

CONTENTS

THE EFFECT OF RAINFALL AND TEMPERATURE ON THE ANNUAL RADIAL GROWTH OF PINE IN THE SOUTHERN UNITED STATES

INTRODUCTION

The basic cause of the rapid growth of pine in the South is generally attributed to the warm, humid climate. Marked fluctuations of annual growth have been observed by almost everyone who has had occasion to make increment borings, or count and measure annual rings on stumps. These fluctuations in annual-ring width can often be correlated with fire damage, decrease in stand density due to cutting, and other factors. However, they are in many instances correlated with the climatic factors, rainfall, and temperature.

The influence of rainfall and temperature upon the radial growth of four species of pine has been evaluated and some of the outstanding correlations are given in this paper. The specific objective of the work was to find a satisfactory method of measuring the relationship between rainfall and temperature and growth, and to present the results of the most acceptable methods of analysis in graphic form and discuss the more outstanding correlations. The species studied and the locations where data were obtained were: loblolly pine (*Pinus taeda* L.) in southwestern Louisiana; slash pine (*P. caribaea* Morelet) and longleaf pine (*P. palustris* Mill.) in southern Georgia; and shortleaf pine (*P. echinata* Mill.) in northern Arkansas. The growth data were obtained by Jesse D. Diller of the Division of Forest Pathology, U. S. Department of Agriculture, while making a reconnaissance survey of pine-canker infection in the South. Diller made all the growth measurements and turned the data over to the writer, who has not seen the specific stands in which trees were measured. The writer is indebted to Professors R. C. Hawley and Ellsworth Huntington of Yale University, and L. H. Reineke of the Northeastern Forest Experiment Station for many helpful suggestions in the analysis.

PREVIOUS WORK

The effect of climatic change on the diameter growth of long-lived trees in semi-arid regions has been the subject of extensive study. The objectives of these studies have been aptly expressed by Douglass (1924, 1934) in the following statement: "The annual rings [of trees] at the dry borders of the southwestern forests give excellent rainfall records. This is a reaction of the tree to its environment and as such is a contribution to ecology. Climatology is closely related to the study of tree rings because long-lived trees give rainfall records for more than a thousand years past and thus supply fun-

damental data unequalled elsewhere in length of time and accuracy of dated record. These long records have developed the use of new and more efficient methods in the study of climatic cycles. These records of rains and droughts also meet the needs of the reclamation engineer, and the soil erosion specialist.

"Geology stands in close relation because the interpretation of modern rings in terms of climate enables us to read the meaning of fossil rings in the study of past climates. The astronomer finds in tree-ring variations a reflection of solar changes over longer periods of time than described in human history. Archaeologists have studied rings in the constructions of primitive man in which are recorded ancient rainfall conditions; by cross identification they are at times able to learn the exact time of construction of great ruins, and can often see in the droughts recorded in the annual rings of timbers a possible explanation of abandonment of habitations."

Douglass (1914, 1922) working with ponderosa pine in Arizona found that (1) variation in the annual rings of individual pine trees, in the dry regions of the northern part of the state, exhibited such uniformity that the rings of one tree could be cross-identified with rings in other trees over large areas and the date of their formation established with practical certainty, and that (2) ring thickness was proportional to rainfall with an accuracy of 70 to 85 per cent in recent years and this accuracy presumably extended over centuries, and (3) an empirical formula could be made to express the relationship between tree growth and rainfall. He found the following cycles in the 500-year record of trees near Flagstaff: an approximate 33-year cycle in the last 200 years, a 20-year cycle and a 11-year cycle in the last 400 years. The 11-year cycle showed marked relationship to the California coast rainfall and temperature, and to the sun-spot curve. He also found a still better agreement between tree growth in northern Germany (Eberswalde) and sun-spot occurrence.

Douglass (1917) observed that trees in dry climates provide a valuable record of rainfall, while trees of wet climates give better records of sun-spot activity (11-year periodicity of sun-spots).

Douglass (1909, 1919) found conifers most suitable for climatic studies because of their wide distribution, the great variety of climates in which they occur, and the prominence of the rings. The chief trees that he used were ponderosa pine, Scotch pine, Douglas fir, and Sequoia. Apparently good evidence was found to show that double rings are caused by spring droughts, and that they are indicative of the distribution of rainfall throughout the year in the southwest. Douglass also pointed to the possibility of using tree records in the intensive study of the location of homogeneous meteorological conditions and in outlining meteorological districts.

Kienholz (1934) found no correlation between meteorological conditions and double maxima in the cambial growth of young red pine in New Hamp-

shire. Cambial growth, measured by the MacDougal dendrograph, began early in May, reached a maximum June 2, decreased slightly and reached a second maximum July 9. He suggested that the first maximum was associated with the development of spring wood and the second maximum with the development of summer wood. Kienholz stressed the importance of stored foods in the rapid building of new wood in the spring. This point should be kept in mind in interpreting the reason for a positive correlation between radial growth rate, and summer rainfall of the previous year in slash pine near Waycross, Georgia.

Bogue (1905) investigated the relation between seasonal and annual growth of 27 shade and fruit trees near Stillwater, Oklahoma. Analyzing growth and climatic data for a 4-year period (1898 to 1901) he found that the month of maximum rainfall was also the month of maximum growth. On the basis of such a short time series this correlation may have been fortuitous. He also measured the rings of 42 trees for a 13-year period (1892 to 1904) at East Lansing, Michigan, and observed that an annual precipitation of 30 to 35 inches gave a ring of 0.11 to 0.15 inch wide, and that abnormally large or small rainfall was evidenced by the tree growth of the following year.

Robbins (1921) studied the relation between the growth rates of oak (largely *Quercus rubra* L., and *Q. imbricaria* Michx.) and rainfall and temperature in Missouri. Annual growth data from 16 trees, which were approximately 100 years old, were compared with climatic data from a station 1 mile away. He found the best correlation between the total rainfall for March, April, May, and June and annual radial growth. This correlation was determined graphically[2] by plotting rainfall and growth over time. Robbins found no relation between precipitation of one year and growth during the next. The average temperature of May and June was negatively correlated with growth as determined graphically. He suggests that the "building material (for new growth in the spring) comes from the assimilatory activity of the leaves and not from reserve foods." This is opposite to the suggestion of Kienholz (1934).

Burns (1929) considered it impossible to correlate ring width with the climatic factors because of the phenomenon of eccentric growth, the variation in width of a single ring at different elevations on the trunk, and the suppression of rings near the base of the tree. He believed that the *source, time,* and *nature* of precipitation was immaterial, but that the essential condition was that available moisture be present around the tree roots during the season when temperature conditions are favorable for growth. Apparently he gave considerable weight' to surface and subsurface lateral movement of water in the soil. The concentration of tree roots in the A horizon of most forest

[2] In the writer's experience it has been extremely difficult, if not impossible, to isolate by graphic means the period of rainfall that shows the best association with growth.

soils indicates to the writer the great importance of an immediate aerial source of soil moisture and not laterally translocated moisture.

The effect of rainfall and temperature on the diameter growth of longleaf pine in western Florida was studied by Lodewick (1930), working in the Choctawhatchee National Forest in western Florida about 7 miles from the Gulf of Mexico. The region receives about 60 inches of rainfall a year, and the soil on which the study-trees were located was deep Norfolk sand. Fifty-seven trees, ranging in diameter from 2 to 19 inches at breast height were measured. The time series involved was 12 years. The data were analyzed by graphic methods. Rainfall during the latter part of the growing season (from June 1 or July 1 until October 15) exerted the principal controlling influence on summer wood formation. Rainfall accompanying the period of spring wood formation showed a fair correlation with the width of the spring wood, but the correlation was poorer than that for the summer wood. He found the width of spring wood over a number of years to be almost constant irrespective of rainfall. Lodewick states "vigorous trees were better visual indicators of the effect of climatic factors on wood production than were non-vigorous trees, since the sinuosities of their growth curves were more marked." This is opposite to the findings of Douglass, although each worked with different trees in different climates. Lodewick found little or no association between temperature and growth.

Exception is taken by Lyon (1935) to the work and conclusions of Burns (1929) because the latter used such a short time series, 12 years, and because of the youthfulness of the trees (white pine under 10 inches in diameter). Lyon's contention is that the growth rings of young trees are complacent, that is, they apparently do not respond to changes in single environmental factors. The inference is that the annual growth of rapidly growing trees is much less affected by deviations of rainfall and temperature than the annual growth of slowly growing trees, which may be true for hemlock in New Hampshire; but it is in opposition to the findings of Lodewick (1930) in western Florida, and to the observations of the writer in Georgia, Louisiana, and northern Arkansas.

Diller (1935) studied the relation of temperature and precipitation to the growth of beech in northern Indiana. He measured the annual growth of 10 trees in each of seven woodlands, and correlated it with climatic data for the period of 1913 to 1933. Annual variations in the width of rings for the period were correlated inversely with the average temperature for the month of June. In some stands a fair correlation was found between annual growth rate and rainfall for June, while in others little correlation existed. He found that drought years resulted in a decrease in growth rate the following year, whereas wet years in most cases resulted in an increase in growth rate the same year.

Cary, Wyman, Harper, and Craighead (1932) recognize the effect of prolonged dry periods in the naval stores region on the vigor of longleaf and slash pines and the consequent yield of gum and also the effect of other factors associated with dry periods such as beetle attack and fire which often result in the death of worked trees or in dry-facing (drying out of wood tissue). They state: "Weather Bureau records rate 1931 as the driest year for many years and the first two months in 1932 have been of much the same character. The ground being dried out very deeply and thoroughly. . . . Only small yield of gum is to be expected while the soil is in this condition; faces will dry in unusual numbers; timber may die in some quantity, the latter being helped by insects." Cary (1932a) observed that longleaf pine on deep sands on ridges suffered more from drought than on soils with clay nearer the surface, and more than slash pine. However, an impenetrable hardpan or claypan near the surface stops the downward growth of the tap root of longleaf pine into the permanent water table. The volume of soil above the pan, in which all the tree roots are necessarily located, is relatively small and cannot hold a great amount of water. On such soils the growth of longleaf pine is markedly reduced by prolonged dry periods (Cary, 1932b).

The advisability of light-working of trees, on severe sites during and immediately after droughts was inferred by Cary (1932c, 1933) who also observed heavy mortality and dry-facing in dense stands of slash pine growing on flat ground and old-field following the dry period of 1931 and 1932.

FIELD METHOD AND DESCRIPTION OF STANDS

The growth measurements were obtained from increment borings at breast height (4.5 feet above the ground). Only trees in relatively open stands were measured in order to eliminate, as much as possible, the effects on annual radial growth of initial stand density and the closing of the crowns with increasing age. However, growth curves indicated that even when this precaution was taken a decreasing trend of growth was usually present. Only one boring was taken from each tree. The work of Lodewick (1930) with longleaf pine shows that growth on one radius is about as reliable as data obtained by averaging the growth of four cores taken on different sides of the same trees.

The annual growth rings were measured in the field with a metric scale or with an engineer's scale but when the latter was used the measurements were later converted to the metric system. By measuring the growth in the field as the trees were bored, possible errors due to shrinkage or contortion of the cores as a result of drying were eliminated.

Dominant trees, usually ten, were measured in each stand. The average height of the trees was estimated, and the age obtained from the increment cores. The diameter of each tree was also obtained with a diameter tape.

Measurements were made during the summer of 1934 and they included the 1933 annual ring; but none of the 1934 ring which was in the process of formation. Ring measurements of the trees in the stand near DeRidder, Louisiana, were made on May 8. In Georgia, all measurements were made between May 30 and June 13 with the exception of the stand located 4 miles west of Soperton, which was measured on September 18. The ring measurements in Arkansas were made on May 22 and May 23.

The nature of the stands and their location follows:

LOUISIANA

DeRidder   Loblolly pine
Location of stand: 4.6 miles south of DeRidder.
Location of weather station: Lake Charles, 40 miles south of DeRidder.
Number of trees: 10. Average age in years: 25.
Average diameter in inches: 11.8. Average height in feet: 60.

GEORGIA

Waycross   Slash pine
Location of stand: 11.8 miles north of Waycross.
Location of weather station: Waycross.
Number of trees: 10. Average age in years: 25.
Average diameter in inches: 7.3. Average height in feet: 40.

Waycross   Longleaf pine
Location of stand: 9.2 miles north of Waycross.
Location of weather station: Waycross.
Number of trees: 10. Average age in years: 17.
Average diameter in inches: 8.8. Average height in feet: 30.

Valdosta   Slash pine
Location of stand: 10.5 miles east of Valdosta.
Location of weather station: Quitman, 30 miles west of stand.
Number of trees: 11. Average age in years: 17.
Average diameter in inches: 8.2. Average height in feet: 30.

Cordele   Slash pine
Location of stand: 18 miles south of Cordele.
Location of weather station: Americus, 30 miles northwest of stand.
Number of trees: 10. Average age in years: 20.
Average diameter in inches: 9.0. Average height in feet: 35.

Cordele   Longleaf pine
Location of stand: 18 miles south of Cordele.
Location of weather station: Americus, 30 miles northwest of stand.
Number of trees: 10. Average age in years: 20.
Average diameter in inches: 8.5. Average height in feet: 40.

Soperton   Slash pine
Location of stand: 11 miles northeast of Soperton.
Location of weather station: Dublin, 25 miles northwest of Soperton.
Number of trees: 10. Average age in years: 18.
Average diameter in inches: 8.9. Average height in feet: 35.

Soperton   Slash pine

Location of stand: 4 miles west of Soperton.
Location of weather station: Dublin, 20 miles northwest of stand.
Number of trees: 50. Average age in years: 9.
Average diameter in inches: 8.1. Average height in feet: 29.

ARKANSAS

Calico Rock   Shortleaf pine

Location of stand: 2 miles southwest of Calico Rock.
Location of weather station: Calico Rock.
Number of trees: 10. Average age in years: 32.
Average diameter in inches: 8.2. Average height in feet: 45.

Madison County   Shortleaf pine

Location of stand: 5 miles west of Eureka Springs.
Location of weather station: Eureka Springs, 10 miles north of stand.
Number of trees: 10. Average age in years: 35.
Average diameter in inches: 7.7. Average height in feet: 45.

Carroll County   Shortleaf pine

Location of stand: 9 miles west of Eureka Springs.
Location of weather station: Eureka Springs, 7 miles west of stand.
Number of trees: 8. Average age in years: 25.
Average diameter in inches: 8.3. Average height in feet: 45.

CLIMATE OF LOCALITIES STUDIED

Climatological data were obtained from weather stations, nearest to the stands studied, whose records were complete for the period of time included in the study. The locations of the weather stations with respect to the stands are given above.
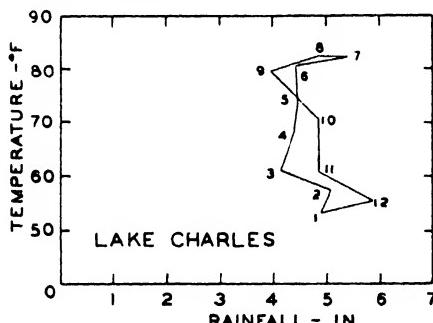
FIG. 1. A climograph for Lake Charles, Louisiana. The average monthly temperature is plotted over the average rainfall for each month. The twelve points are connected by straight lines in chronological order. The figure is based on monthly averages for the 16 years from 1918 to 1933 for which growth data are available. Variation in rainfall due to differences in the number of days in each month was adjusted by correcting the monthly averages to a 30-day month. The numbers on the climograph indicate the month, 1 for January, 2 for February, etc.

SOUTHERN LOUISIANA

The character of the climate of southwestern Louisiana can best be understood by examining the climograph for Lake Charles (Fig. 1). The average annual rainfall at Lake Charles is 57 inches and the average annual temperature is 68° F. The climograph is a convenient form to show graphically the climate of a place. It is constructed by plotting the average temperature of each month over the average rainfall and connecting the points by lines in their chronological order. The points representing each month are num-

bered beginning with January as 1, February as 2, and so on. The climograph shows the monthly distribution of rainfall and monthly temperature for the 16 years from 1918 to 1933. The average monthly rainfall is between 4 and 6 inches; and the average monthly temperature ranges from 53° F. in January (number 1) to 84° F. in August (number 8), a total mean range of 30°. The lowest rainfall occurs in March (number 3) and September (number 9), and the heaviest rainfall comes in December (number 12) and July (number 7).

SOUTHERN GEORGIA

The average annual rainfall for Waycross is 48 inches; and the average annual temperature is 68° F., the same as Lake Charles, Louisiana. Figure 2 shows average monthly distribution of rainfall and the average monthly temperatures. The range of monthly rainfall is from 2 to over 7 inches, and the range of average monthly temperature is from 53 to 82° F. October (number 10) and November (number 11) are the driest months, with about 2 inches of rainfall, while July (number 7) has over 7 inches. July and August (number 8) are the two warmest months with average temperatures of 81 and 82° F., respectively. The average rainfall for the spring months, March, April, and May (number 3, 4, and 5) is relatively low and fluctuations of rainfall for these months are often reflected in the growth of pine.

There is a relatively large increase in temperature from March to April (numbers 3 to 4). These two points should be kept in mind in interpreting the reason for the high association between annual radial growth and the two climatic factors for the early spring period.
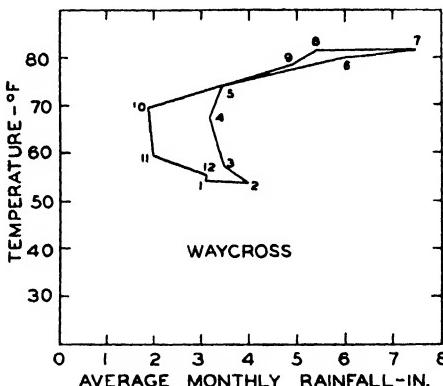
Fig. 2. A climograph for Waycross, Georgia. Average monthly temperature is plotted over the average monthly rainfall. The figure is based on averages for the 17 years from 1917 to 1933 corrected to 30-day months. Waycross is located in the extreme southern part of the state. The range of average monthly temperatures is approximately the same as for southern Louisiana, but the rainfall distribution is characterized by a definite dry period in October and November, and a rainy season through June, July, and August. The heavy summer rain is partly monsoonal from the Gulf, and partly convectional.

· NORTHERN ARKANSAS

The average annual rainfall for Calico Rock is 41 inches; and the average annual temperature is 59° F. which is 9° lower than for southern Louisiana and southern Georgia. As can be seen in Figure 3 the range of average monthly rainfall is from about 2.5 inches in February (number 2) to 5 inches in April (number 4), while temperature ranges from 38° F. in January (number 1)

to 81° F. in August (number 8). Rainfall is relatively low in the winter and early spring and high in April and May (numbers 4 and 5).

Calico Rock is on the Ozark Plateau in the northern and central part of the state. The range of average monthly temperatures is greater than at Lake Charles, Louisiana, being between 40 and 45° F. The heaviest rainfall occurs in April and May (numbers 4 and 5), while the lowest occurs in February (number 2). Total rainfall for Calico Rock is approximately 44 inches a year.

ANALYTICAL METHODS

Growth data for DeRidder, Louisiana, and climatic data for Lake Charles were correlated by graphic methods in which the average annual growth of 10 trees was plotted over the year in which the growth took place— 1918 to 1933—and the points connected by straight lines. The rainfall for two periods, January to June and July to December, inclusive, were then plotted over time above the growth curve. No consistent relationship appeared to exist between growth and rainfall for either of the two periods. Average periodic temperature and growth compared in a similar manner failed to show definite and consistent relationship. It was then decided to use moving totals of rainfall by 3, 4, and 5-month periods; and moving averages of temperature for the same periods. These climatic data were plotted over time and the fluctuations of the curves connecting the points were compared with the annual fluctuations of the growth curve. Definite positive relationship was seen to exist between rainfall for certain of the early spring periods and growth. However, it was impossible by the graphic method alone to determine whether the rainfall of January to May, inclusive, or February to June, inclusive, was most clearly associated with growth. Many graphs of this type were made for the loblolly pine data from near DeRidder, Louisiana, and the slash pine data obtained near Waycross, Georgia, before it was finally decided that a mathematical method of measuring degree of association between the climatic factors and growth was necessary.

Other investigators, Douglass, Huntington, and Diller, have used the correlation coefficient[3] to measure the relationship between each of the climatic factors and growth in a time series.

[3] Correlation coefficient: $r = \dfrac{S(xy)}{Sx^2 \cdot Sy^2}$, Fisher (1934) where S = sum, x = deviation of either rainfall or temperature, and y = the percentage deviation of annual growth.

The chief objection to the use of the correlation coefficient in the measurement of degree of association in a time series, is that we must assume that the relationship between the two variables (rainfall or temperature and growth) is linear. This objection, often raised by statisticians, is well founded. A linear relationship is one that can best be expressed by a straight line. For radial growth and rainfall correlation, equal increases or decreases in rainfall are associated with proportional deviations in growth. Almost everyone will agree that in general the relationship of growth to rainfall is curvilinear; increases in rainfall up to a certain amount will result in proportionate increases in growth, but above that amount continued increases in rainfall will not result in increases in growth to the same degree; finally, a point in the increase of rainfall may conceivably be reached where there is actually a diminution of growth.

The point under discussion is illustrated in Figure 4. Given the hypothetical curve of annual growth over rainfall A B C D in which the relationship between the two variables, considered as a whole is curvilinear; any group of growth and rainfall data that could be represented by the segment A B has a linear relationship which could be measured by the correlation coefficient. Such a correlation would be positive. If the data were represented by the segment B C the correlation coefficient would indicate no association, when actually a relationship does exist but it is curvilinear. By the same method, data represented by the segment C D would give a negative correlation coefficient.

In this study it has been assumed that, with the species concerned, and the climate, soils, and topographic positions of the areas, rainfall has never been excessive for the periods involved, and that the relationship between radial growth and either of the two climatic factors can best be represented by a

FIG. 4. The probable curvilinear relationship between annual radial growth and rainfall.

straight or nearly straight line. With this assumption the correlation coefficient has been used to measure association between growth and the climatic factors.

The standard error of the correlation coefficient was not used because of the short time series involved; that is, the small number of samples employed when temperature, or rainfall, and growth are considered one variate. The time series vary from 7 to 17 years, which means a sample of 7 to 17 variates. The statistical significance of the correlation coefficient for small samples can

best be determined by the use of Fisher's table of the values of the correlation coefficient for different levels of significance. Correlation coefficients falling in the 0.02 level of significance, or less, were considered statistically significant in all of the following analyses; this level of significance means that the probability of the correlation arising, by random sampling, from an uncorrelated population is only 2 out of 100.

ANALYSIS OF DATA

SOUTHERN LOUISIANA

When the average annual radial growth of the 10 loblolly pine trees near DeRidder, Louisiana, was plotted over time, and a straight line fitted to the points, it was evident that the growth rate was decreasing (Fig. 5). Total rainfall for all groups of months showed no such decreasing trend. In fact the smoothed curve of rainfall for January to April, inclusive, was horizontal (this curve is not shown in Fig. 5, but rather the actual rainfall is represented by broken lines). Since rainfall over the 16-year period was not decreasing, it was evident that the decreasing trend of growth rate was due to some other factor, or factors, than cyclic change of climate; the most likely factor being the closing of the stand as it grew older (it was 25 years old in 1933). By using the deviations of the average annual growth from the curve of growth the effects of the decreasing trend were eliminated. The use of the actual deviations of average annual growth from the 16-year arithmetic average would have eliminated almost entirely the effects of annual fluctuations of periodic rainfall and temperature. The average annual growth for the 10 trees from 1918 to 1933 was 6.4 mm. Had the deviations of the average growth for each year been calculated from this figure, there would have been a preponderance of positive deviations in the first part of the time series and a preponderance of negative deviations in the last part. The correlation coefficient calculated from these deviations would have shown little or no association between growth and the climatic factors, when actual association exists. Since the effects of the downward trend of growth were eliminated by the use of the annual percentage deviations from the best straight line that could be fitted to the data, this analysis is concerned with the effects of annual fluctuations of periodic rainfall and temperature on annual growth, and not with the effects of cyclic change, which might be reflected in secular trend of growth.

The correlation coefficients for growth and rainfall, and for growth and temperature were determined by using monthly rainfall and average temperature for March, April, May, and June, and the annual percentage deviation of growth from the growth curve (Table 1). The highest correlation between radial growth and monthly rainfall was found for May, the correlation coefficient being +0.557, which is statistically significant, according to Fisher's
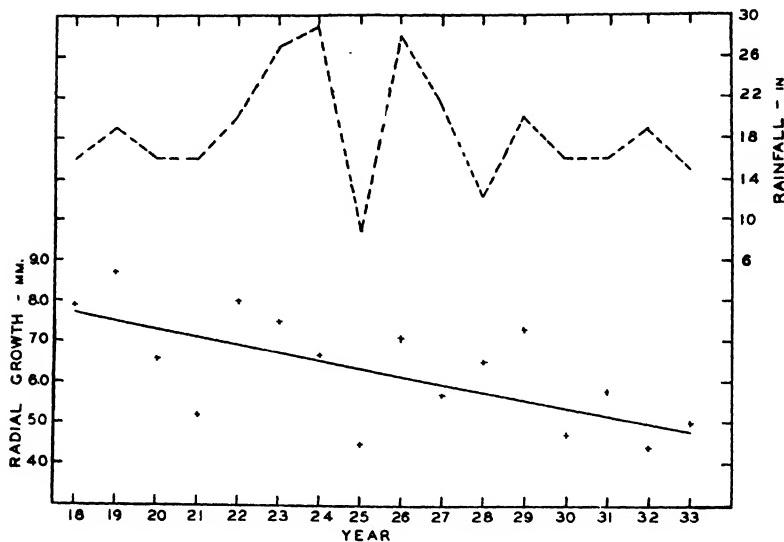
FIG. 5. The relation between radial growth of loblolly pine at DeRidder, Louisiana,
and rainfall at Lake Charles, Louisiana. The solid line shows the trend of radial
growth of 10 trees from 1918 to 1933. The broken line shows the fluctuations of the
total rainfall during January to April, inclusive, for the same years. The growth curve
was fitted by the method of least squares and shows a downward trend, while a smoothed
curve of rainfall (not shown) maintains an even trend.

table of levels of significance. Correlation coefficients for the other months
were not statistically significant. Average monthly temperature showed little
correlation with growth. When the deviations of the rainfall by 4-month
periods were correlated with growth, rainfall for February to May was found
to give the highest correlation coefficient, +0.479, but it is not statistically
significant. The highest negative correlation of temperature and growth was
for the same 4-month period (Table 2).

The curve of correlation coefficients for 4-month periods indicates by its
slope that the rainfall in May has more influence on growth than rainfall dur-
ing the previous December (Fig. 6); on the basis of this observation the cor-
relation coefficients for 5-month periods of rainfall and growth were cal-
culated; in which, the rainfall for January to May, inclusive, of the current
year was found to have a relatively high positive correlation with growth,

TABLE 1. The relation of annual radial growth to rainfall and temperature of single
months as measured by the correlation coefficient, DeRidder, Louisiana.[4]

Growth with:	Month			
	March	April	May	June
Rainfall..................	....	+0.275	(+0.557)[s]	—0.027
Temperature..............	(—0.216)	—0.100	+0.003	+0.153

[4] Based on the growth of 10 trees from 1918 to 1933.

TABLE 2.   The relation of annual radial growth to rainfall and temperature for four-month periods as measured by the correlation coefficient, DeRidder, Louisiana.[5]

Growth with:	Oct., Nov., Dec., Jan.	Nov., Dec., Jan., Feb.	Dec., Jan., Feb., Mar.	Jan., Feb., Mar., Apr.	Feb., Mar., Apr., May	Mar., Apr., May, June	Apr., May, June, July	May, June, July, Aug.
Rainfall.......	+0.122	+0.101	+0.420	+0.454	(+0.479)[5]	+0.367	+0.342	+0.196
Temperature....	....	....	....	—0.463	(—0.470)	—0.210	....	......

[5] In Tables 1 to 7, inclusive, values in parentheses are the highest, and values in italics are statistically significant.   According to Fisher's tables of values of correlation coefficients for different levels of significance, the probability of this correlation arising, by random sampling, in an uncorrelated population is 2 in 100 or less.
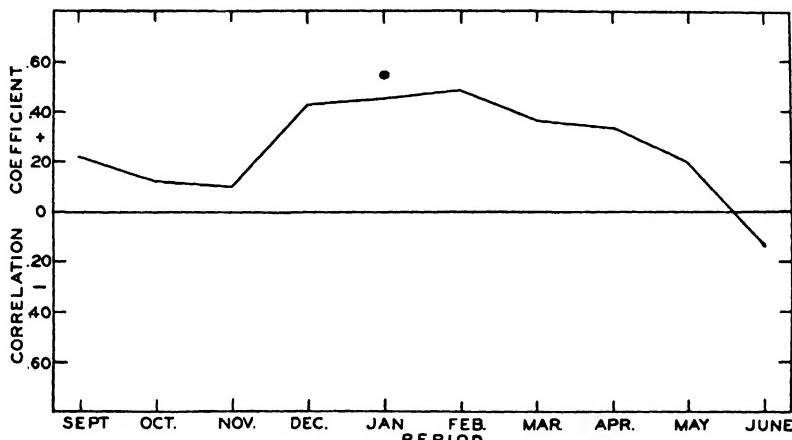
FIG. 6.   The association between the annual radial growth of 10 loblolly pine trees near DeRidder, Louisiana, and rainfall for 4-month periods at Lake Charles, Louisiana, as measured by the correlation coefficient.   The period is indicated by the abbreviation of the first month, i.e., Sept. = September, October, November, and December of the year previous to which the growth was made, while Jan. = January, February, March, and April of the year in which the growth was made.   The inscribed cross indicates the correlation coefficient for growth and rainfall during January to May, inclusive.

$r = + 0.545$ (Table 3).   This value is just under the minimum for statistical significance.   The correlation coefficient for January to May is given in Figure 6 as an inscribed cross showing its relation to the values for the shorter climatic periods.

TABLE 3.   Correlation coefficients indicating the relation of annual radial growth to rainfall and temperature for five-month periods, DeRidder, Louisiana.[6]

Growth with:	Previous Year		Current Year			
	January to May	February to June	December to April	January to May	February to June	March to July
Rainfall.......	(—0.559)	+0.394	+0.394	+0.545	+0.431	......
Temperature....	....	......	—0.388	—0.421	(—0.445)	—0.240

[6] Based on the growth of 10 trees from 1918 to 1933.

The relation of total rainfall and average temperature of January to May, inclusive, to growth is shown on logarithmic scale in Figure 7. In this graph the radial growth is corrected for a decreasing trend, while temperature and rainfall do not exhibit a decreasing trend. Positive fluctuations of rainfall are seen to be associated with positive fluctuations of growth while positive fluctuations of temperature are associated with average or less than average growth. The low rainfall in 1921 and 1925, particularly the latter, was reflected markedly in the growth rate. The temperatures for these two years were above average. High temperature in 1927 was associated with a decreased growth rate although rainfall was slightly above the average. The low rainfall of 1928 was in part offset by the low temperature, and growth increased over the previous year. The lack of positive correlation between rainfall and growth in 1931 and 1933 can probably be attributed to inverse variation in temperature. Low temperature and low rainfall in 1931 were associated with an increase in growth over the previous year, while an increase in temperature and a slight increase in rainfall in 1932 was associated with a decrease in growth. Of particular interest in Figure 7 is the low range of temperature, only about 7° F. However, only slight rises in temperature in April and May are associated with low growth in 1921 and 1927.

Smoothed curves of growth and rainfall show positive agreement in their fluctuations. The curves were left unsmoothed in Figure 7 in order to bring out the magnitude of the annual fluctuations.

The relation of the percentage deviation of the annual growth to the de-
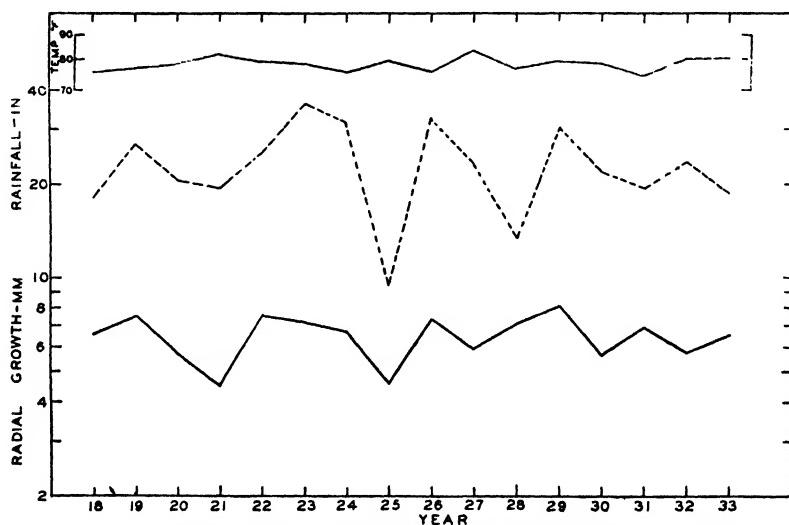
Fig. 7. The relation of total rainfall and average temperature during January to May, inclusive, at Lake Charles, Louisiana, to the growth of loblolly pine near De-Ridder, Louisiana. The lower solid line represents growth corrected for decreasing trend due to the closing of the stand. The broken line represents total rainfall during January to May, inclusive. The upper solid line shows the trend of average temperature for the same period. Growth, rainfall, and temperature are plotted on logarithmic scale.

viation of the rainfall is shown in Figure 8, left side. The trend line indicates the strength of the association. During the 8 years in which the rainfall for January to May, inclusive, was above average, growth was above average 7 years; while of the 7 years when rainfall was below average, growth was below average 4 years. On the right, in Figure 8, a similar graph of percentage deviation of growth and the deviation of the average temperature is shown. In the 8 years in which temperature was below average, growth was above average 7 years; while in the 8 years that temperature was above average, growth was below average 5 years. Considering the two graphs together, low rainfall and high temperature account for nine of the combinations when growth was less than average.
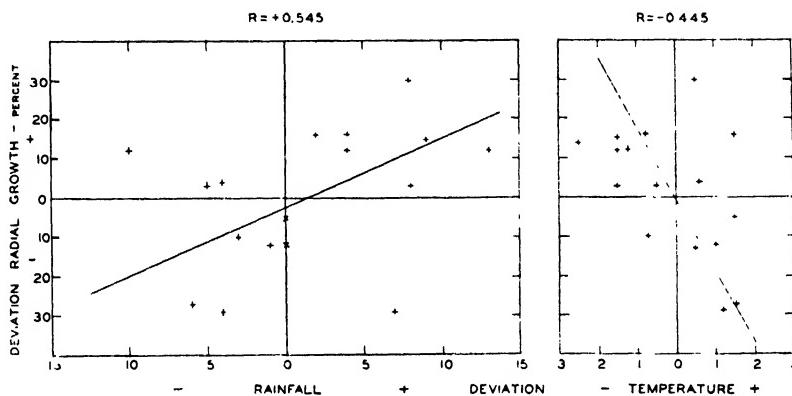
FIG. 8. Relation of growth of loblolly pine, DeRidder, Louisiana, to rainfall (left) and to temperature (right). The percentage deviation of the average annual growth of 10 trees from their trend line is plotted over the deviation from the average of the annual precipitation of January to May, inclusive. The graph on the right is based on the same growth data plotted over the deviation of the average temperature from the average periodic temperature of the entire time series, 1918 to 1933. Both lines were fitted on the basis of the dependent variable, growth.

The three variables, growth in percentage of the average based on the curve, total rainfall for January to May, inclusive, and average temperature for the same period, are brought together in Figure 9. Growth in percentage of the average for each year was plotted on the total rainfall and average temperature, and smooth lines (isopleths) fitted to the points at 5 per cent intervals (points are not shown). In general, if the lines in such a chart are parallel to the temperature axis that variable has little influence on growth, which in such a case would vary with rainfall. The opposite extreme would be for the isopleths to be distributed parallel to the rainfall axis in which case growth would vary with temperature. Although Figure 9 is based on only 16 points (16 years), an intermediate condition to the two outlined above obtains. The heavy line, 100 per cent isopleth, indicates conditions of average growth. This isopleth shows that growth remains average if temperature increases rapidly with increases of rainfall, while if rainfall remains constant and temperature increases, annual growth will decrease. Annual growth re-

mained average when rainfall and temperature increased from 12 inches and 64° F., respectively, to 22 inches and 69° F, respectively. The highest annual growth occurred when periodic rainfall was between 20 and 30 inches with the temperature between 64 and 67° F. However, the supporting data are insufficient for this to be considered the climatic optimum.

SOUTHERN GEORGIA

The growth of 10 slash pine trees near Waycross, Georgia, during 1918 to 1933 showed a trend of increasing growth. There was no reason to believe that the same rainfall period as

FIG. 9. The relation of both rainfall and temperature to growth of loblolly pine, DeRidder, Louisiana. The annual growth expressed as a percentage of the average is plotted on the total rainfall and average temperature for February to May, inclusive, of each year. Isoplethic lines (as contour lines) were fitted to the percentage values at 5 per cent intervals. The heavy line (100) indicates climatic conditions associated with average radial growth rates.

The isoplethic lines indicate that both rainfall and temperature for February to May, inclusive, have an influence on growth rate for the current year. Average growth rate is maintained if increases in temperature are accompanied by increases in rainfall.

in southwestern Louisiana (January to May, inclusive) would have the highest correlation with the growth of slash pine in southern Georgia. It was necessary to follow a similar procedure in eliminating months and groups of months to find the one in which the climatic factors were most closely associated with radial growth. This was accomplished, as before, by using climatic data for single months and groups of months (averages in the case of temperature) in correlation with growth. The correlation coefficients for single months and groups of months are shown in Table 4. The correlation coefficient for annual growth and the rainfall of February to April, inclusive, is higher, +0.750, than for single months or longer periods. This value is statistically significant.

TABLE 4. Correlation coefficients showing the relation of annual radial growth of slash pine to monthly and periodic rainfall near Waycross, Georgia, based on the growth of 10 trees from 1918 to 1933.

January	February	March	April
+0.113	(+0.670)[7]	+0.517	+0.243
December, January, February	January, February, March	February, March, April	March, April, May
+0.432	+0.710	(+0.750)	+0.443

December, January, February, March	January, February, March, April	February, March, April, May
+0.570	(+0.730)	+0.625
December, January, February, March, April	January, February, March, April, May	February, March, April, May, June
+0.466	(+0.668)	+0.507

[7] See footnote 5.

The apparent sensitivity of the annual radial growth of slash pine near Waycross, Georgia, to the spring rainfall of the year in which the growth took place suggested the possibility of determining the effect of the previous year's rainfall and temperature on current annual growth. This was done by calculating correlation coefficients for rainfall and growth, and temperature and growth by 3-month moving climatic periods beginning with January to March, inclusive, of the year previous to that in which the growth was made. Ten periods of the previous year and 11 periods of the current year were used. The results are shown in Table 5, and the correlation coefficients are plotted in Figure 10. The effect of early spring rainfall on growth is evidenced by the high positive correlation for January to March, inclusive, and February to April, inclusive, of the current year. The effect of rainfall during the years previous to those in which the growth occurred is brought out by the relatively high positive correlation between growth and the rainfall of the previous summer. This may be due to the effect of favorable, or unfavorable, rainfall during the summer and late summer on the elaboration and storage of foods that are used in the rapid building of new woody tissue the following spring.

A relatively high negative correlation exists between the average temperature of July to September of the previous year and growth, while the average temperature of June to August of the current year has a still higher negative correlation with growth, the correlation coefficient being —0.800, which is statistically significant. The correlation analysis clearly indicates that rain-
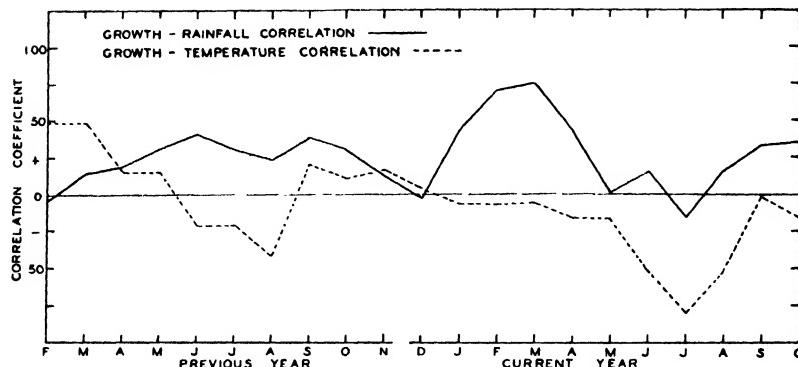
FIG. 10. The association between annual radial growth of slash pine and rainfall and temperature for 3-month periods at Waycross, Georgia, as measured by the correlation coefficient. The period is indicated by the first letter of the second month (F = period of January, February, and March). The 10 periods on the left half of the figure are for the year previous to the one in which the growth took place, and end with the period of October to December of the previous year. The current year correlation begins with the period of November and December of the previous year plus January of the current year.

fall in the early spring and temperature in the summer are closely associated with radial growth.

A graphic representation of the strength of association between radial growth and the rainfall of February to April is given in Figure 11. The percentage deviation of the annual growth is plotted over the annual deviation of

TABLE 5. The relation between the annual radial growth of slash pine for 16 years and the two climatic factors, Waycross, Georgia.

Period	Correlation coefficients for radical growth and	
	Rainfall	Temperature
January, February, March	−0.027	0.485
February, March, April	0.136	0.492
March, April, May	0.193	0.151
April, May, June	0.306	0.155
May, June, July	(0.414)	0.218
June, July, August	0.302	−0.218
July, August, September	0.235	(−0.415)
August, September, October	0.398	0.216
September, October, November	0.317	0.115
October, November, December	0.137	0.162
November, December, January	−0.078	0.027
December, January, February	0.432	−0.064
January, February, March	0.710	−0.053
February, March, April	(0.750,[8]	−0.043
March, April, May	0.443	−0.154
April, May, June	0.045	−0.168
May, June, July	0.156	−0.506
June, July, August	0.154	(−0.800)
July, August, September	0.155	−0.524
August, September, October	0.338	−0.020
September, October, November	0.357	−0.165

[8] See footnote 5.
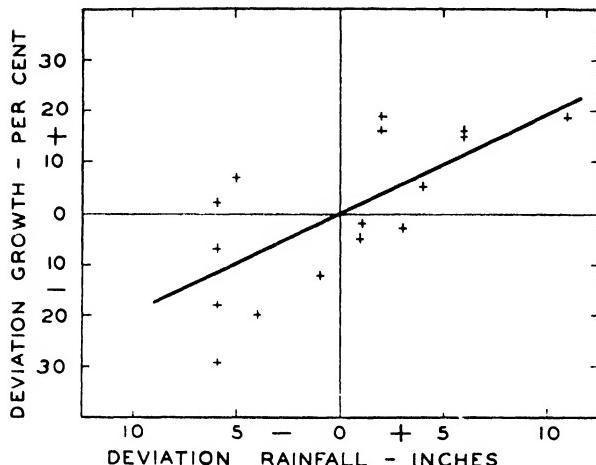
FIG. 11. The relation between the percentage deviation of annual growth of slash pine from the trend line and the deviation of annual rainfall from the average of **February to April**, Waycross, Georgia. The line representing the trend was fitted to the points on the basis of the dependent variable, growth; based on the average annual growth of 10 trees for 16 years.

periodic rainfall from the mean. A horizontal curve would indicate no relationship between growth and rainfall. A decrease in the rainfall during February to April, inclusive, of 5 inches below the average results in a deviation of growth from the average of 10 per cent, while an increase in periodic rainfall of 5 inches above average is associated with an increase in growth of 10 per cent.

The correlation coefficients indicate that rainfall during February to April, inclusive, is most influential in determining the amount of growth. The rainfall for this period is plotted over years in Figure 12 with the annual growth corrected for an increasing trend.

The annual growth of slash pine near Waycross, Georgia, shows the closest agreement with rainfall (February to April, inclusive) of any of the
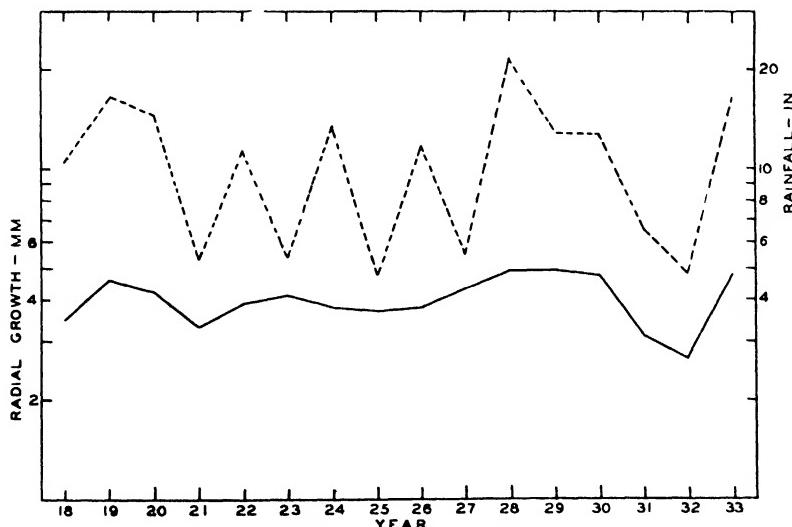
FIG. 12. The relation of total rainfall during February to April, inclusive, to annual growth of slash pine near Waycross, Georgia. The lower solid line is for annual growth corrected for a slight increasing trend. The broken line is for periodic rainfall. Both growth and rainfall are plotted on logarithmic scale.

stands studied. If the annual fluctuations of rainfall for the years 1921 to 1927, inclusive, are disregarded, almost complete agreement with growth obtains. High rainfall and growth in 1919, 1920, 1928, 1929, 1930, and 1933; and low rainfall and growth in 1921, 1931, and 1932 are conspicuous (Fig. 12). Smoothed curves of the two variables follow similar trends almost completely.

An isoplethic chart of growth on rainfall and temperature for February to April indicates that growth varies with rainfall, and that temperature at that time has little influence (Fig. 13). This is to be expected since the correlation coefficient for growth and temperature in only —0.043, which for practical purposes indicates no correlation. Rainfall of 12 inches or more is reflected in average or above average growth.

The extremely low growth of longleaf pine in 1931 and 1932 near Waycross, Georgia, coincides with a similar feature in the growth of slash pine in the same locality. The annual growth of slash pine near Valdosta, Georgia, and rainfall for February to April, inclusive, are shown in Figure 14.

FIG. 13. The effect of total rainfall and average temperature during February to April, inclusive, on the annual growth rate of slash pine near Waycross, Georgia, as illustrated by an isoplethic chart. The chart was made by plotting the annual growth as a percentage of the average on the points representing the total rainfall and average temperature of February to April of each year. Smooth lines (isopleths) at 5 per cent intervals were fitted to the points. The isopleths indicate that radial growth is directly associated with rainfall for the period; and that it is affected but little, if at all, by the range of temperatures that obtained for the period from 1917 to 1933.

Rough agreement obtains between rainfall and growth. Notable features are the low rainfall and growth in 1925, 1931, and 1932; and the high rainfall and growth in 1919, 1920, 1923, 1928, 1930, and 1933. The correlation coefficient for annual growth and rainfall during February to April, inclusive, is +0.540, which is higher than that for the overlapping periods on either side (Table 6).

TABLE 6. The relation between annual radial growth and the rainfall of 3-month periods in Georgia as measured by the correlation coefficient.

Location	Species	Time Series Years	Growth—Rainfall Correlation			
			January February March	February March April	March April May	April May June
Valdosta..	Slash pine.....	16	0.273	(0.540)	0.433	0.052
Waycross..	Longleaf pine..	13	0.404	(0.514)	0.138	—0.115
Waycross..	Slash pine.....	16	0.710	(0.750)[9]	0.443	.....
Soperton .	Slash pine.....	7	0.618	0.566	0.486	(0.649)
Cordele...	Longleaf pine..	12	-0.161	0.213	(0.259)	0.159
Cordele...	Slash pine.....	12	0.251	0.515	(0.523)	0.416

[9] See footnote 5.

This value is not statistically significant as measured by the criterion previously used, but it is close, being only 0.030 below the minimum correlation coefficient that is considered significant.
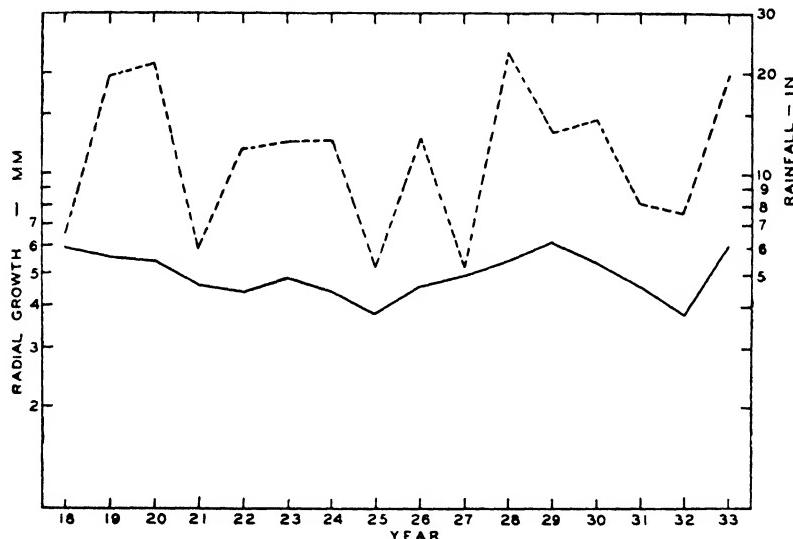
FIG. 14. The relation of rainfall from February to April, inclusive, to the annual growth of slash pine near Valdosta, Georgia. The lower solid line represents annual growth corrected for a slight increasing trend. The broken line represents periodic rainfall. Both growth and rainfall are plotted on logarithmic scale.

The highest correlation coefficient was obtained for the annual growth of 50 slash pine trees near Soperton, and the rainfall of April to June, inclusive. The correlation coefficient for that period was +0.649. The value for January to March, inclusive, +0.618, was also high. Both values fall below the minimum for statistical significance previously used because of the few years involved. Temperature during April to June, inclusive, had the highest negative association with the growth of these trees, the correlation coefficient being —0.413.

Rainfall during February to April or March to May appears to have about equal influence on the growth of slash pine near Cordele, Georgia; the correlation coefficients being +0.515 and +0.523, respectively. A slight positive correlation between growth and temperature during January to February and April to June is apparent. The coefficients being +0.360 and +0.354, respectively (Table 7).

TABLE 7. The relation between annual radial growth and the average temperature of 3-month periods in Georgia as measured by the correlation coefficient.

Location	Species	Time Series Years	Growth—Temperature Correlation			
			January February March	February March April	March April May	April May June
Valdosta..	Slash pine.....	16	0.303	(—0.209)	0.033	0.082
Waycross..	Longleaf pine..	13	0.154	0.120	0.355	(—0.141)
Waycross..	Slash pine.....	16	—0.053	—0.043	0.184	(—0.145)
Soperton..	Slash pine.....	7	0.203	—0.223	0	(—0.413)
Cordele....	Longleaf pine..	12	0.225	—0.161	(—0.331)	0.121
Cordele....	Slash pine.....	12	(0.360)	0.246	0.038	0.354

The combined effects of both rainfall and temperature on the growth of slash pine and longleaf pine in Georgia is shown in Figure 15. This is a composite isoplethic chart of climatic data for the period of February to April from four weather stations, and the percentage deviation of the average annual radial growth from the growth curves of both species. The chart is based on growth of 110 trees in 7 different stands and on time series of from 7 to 18 years.

The isopleths indicate that temperature has little influence on growth, with the possible exception of a slightly beneficial effect of high temperature during the early spring. Growth is influenced markedly by rainfall, average growth being associated with approximately 12 inches of precipitation. Rainfall of between 12 and 20 inches results in greater than average growth, while more than 20 inches of rain apparently causes a decrease in growth rate on the whole. However, the writer is inclined to minimize the apparent decrease in growth when the rainfall is greater than 20 inches on the basis that a heavy rainfall in the spring is often followed by a dry summer with high temperatures, which tend to counterbalance the beneficial effects of the heavy spring rainfall. Periods of heavy spring rainfall are often preceded by a relatively dry late winter which tends to lessen the effects of an abundant rainfall in the spring. These conditions were generally apparent to the writer while tabulating and analyzing the climatic data. Likewise, a very dry and hot late summer will probably cause less foods to be stored and in that way influence the growth the next spring irrespective of the current climatic conditions.
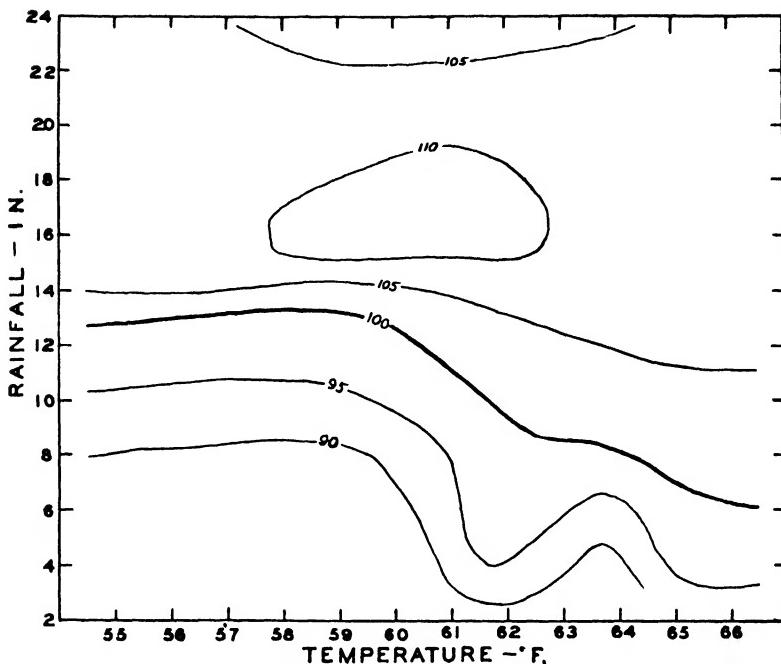
FIG. 15. A composite isoplethic chart for both slash pine and longleaf pine in the coastal plain of Georgia. Growth in percentage of the average for each year was plotted on the points representing the total rainfall and average temperature for February to April, inclusive, of each year. Smooth lines (isopleths) at 5 per cent intervals were then fitted to the points. The isopleths indicate climatic conditions associated with similar growth rates. The chart is based on 110 trees of 2 species; periods of from 7 to 16 years; and climatic data from 4 stations. The isopleth of 110 per cent growth indicates most favorable conditions of rainfall and temperature.

NORTHERN ARKANSAS

The rainfall for April to June, inclusive, has the highest positive correlation with annual growth of shortleaf pine near Calico Rock, Arkansas. The correlation coefficient was $+0.328$, which is not statistically significant. Temperature shows little correlation with growth (Fig. 16).

An 18-year time series was possible with the data from Madison County, Arkansas. The highest positive correlation between growth and rainfall was again found for the period of April to June, inclusive, for which the correlation coefficient is $+0.574$, which is statistically significant. The greatest negative correlation between growth and temperature was found for May to July, inclusive, for which the correlation coefficient is -0.422 (Fig. 17). The effect of above-average temperatures in the late summer was to decrease growth also. Low rainfall was reflected in decreased growth in 1920, 1922, 1926, 1930, and 1931, while high rainfall was associated with greater than average growth in 1927, 1928, and 1929.

The correlation coefficients for the growth of shortleaf pine near Eureka Springs in Carroll County, Arkansas, and rainfall indicate that rainfall from
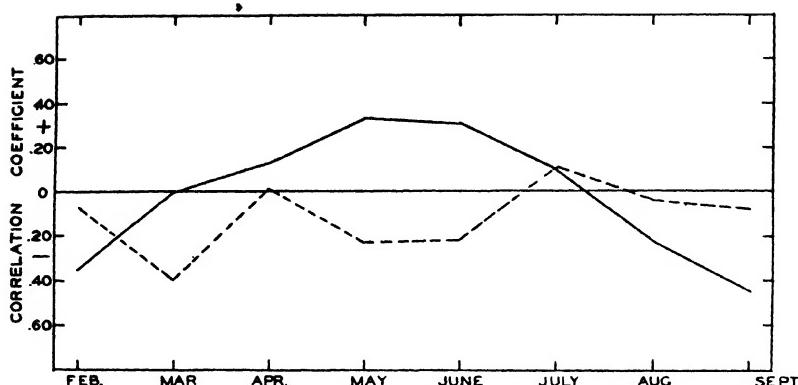
FIGURE 16
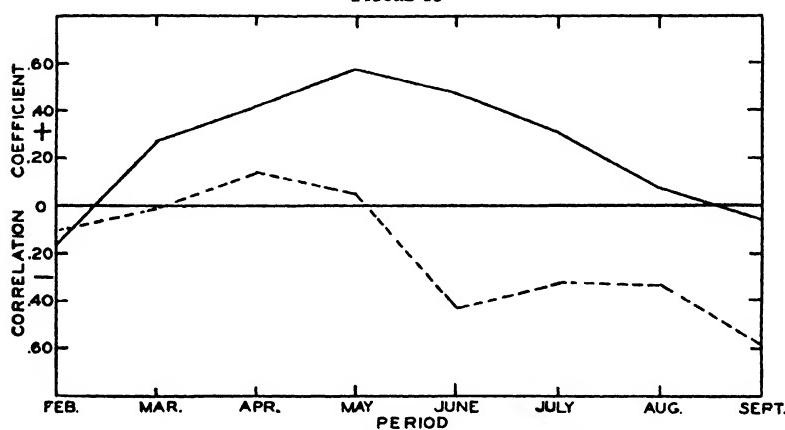
FIGURE 17
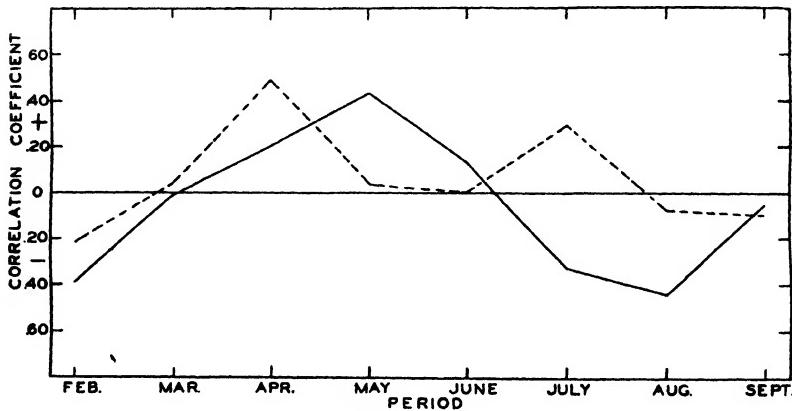
FIGURE 18

FIGS. 16, 17, and 18. The association between annual radial growth of shortleaf pine and rainfall and temperature for 3-month periods at Calico Rock (Fig. 16), and in Madison (Fig. 17), and Carroll (Fig. 18) counties, Arkansas, as measured by the correlation coefficient. Rainfall and temperature data from Eureka Springs were correlated with growth in Madison and Carroll counties. The period is indicated by the middle month, i.e., Feb. = January, February, and March of the year when the growth took place. The solid line is for growth-rainfall correlation and the broken line is for growth-temperature correlation.

April to June is again most closely associated with growth; the correlation coefficient is +0.434 (Fig. 18). However, temperature for the periods of March to May and June to August have a positive association with growth. The correlation coefficients are +0.487, and +0.293, respectively. None of the above correlation coefficients are statistically significant. On the basis of present information the writer does not attempt to explain the positive temperature correlation, except to point out that low temperatures during the growing season may be of such magnitude as to cause a decrease in growth especially in stands on certain topographic positions, relatively moist sites or northern slopes.
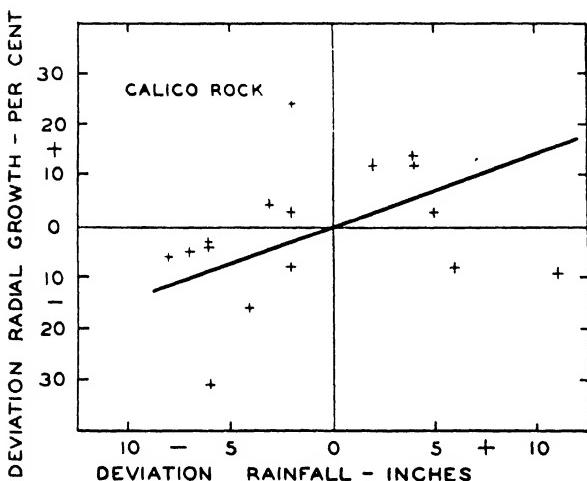
FIG. 19. Relation between the percentage deviation of the annual growth from the trend line of 10 trees near Calico Rock, and the annual deviation of rainfall from the average during April to June, inclusive. The line showing the association was fitted to the points on the basis of the dependent variable, growth. The correlation coefficient for growth and rainfall is + 0.574, and is statistically significant.

The relation of percentage deviation of annual growth to the deviation of rainfall for April to June, inclusive, is given in Figures 19, 20, and 21. Figure 19 is for the stand near Calico Rock, Figure 20 is for the stand in Madison County, and Figure 21 is for the stand in Carroll County. The correlation coefficients for growth and rainfall of these distributions are +0.544, +0.328, and +0.487, respectively.

Of the 10 years when rainfall was below average at Calico Rock, growth was less than average 7 years, and of the 7 years when rainfall was above average, growth was above average 5 years (Fig. 19).

The data for the stand in Madison County do not indicate as good agreement between rainfall and growth as do the data for the stand near Calico Rock (Fig. 20). During the 11 years when rainfall was below average, growth was below average 6 years, and of the 5 years when rainfall was above average, growth was above average 4 years. Of the 11 years when the periodic rainfall was below the average, the growth of trees in the stand in Carroll County was below average 6 years, and of the 4 years when rainfall was above average, growth was above average 3 years (Fig. 21).

The relation between both rainfall and temperature, and annual growth is shown in the composite isoplethic chart for the 3 stands (Fig. 22). This

T. S. COILE

chart is based on the average growth rates of 28 trees in 3 stands and climatic data from 2 weather stations for 17 years. The climatic period is April to June, inclusive. Positive association between early spring temperature and annual growth in the stand in Carroll County (Fig. 18) and in the stand in Madison County (Fig. 17) is reflected in the downsweep of the isopleths when the total rainfall was under 16 inches, and the average temperature increased from 66 to 70° F. Average and above average growth is associated with rainfall of 14 inches and more.

FIG. 20. Relation between the percentage deviation of the annual growth of 10 trees in Madison County from the trend line and the annual deviation of rainfall from the average in April, May, and June at Eureka Springs. The correlation coefficient for growth and rainfall is + 0.328, which is not statistically significant.

SUMMARY AND CONCLUSIONS

An analysis of the relation between the annual radial growth of the 4 southern pines and periodic rainfall and temperature was made for 148 trees in 9 localities and 11 stands in Louisiana, Georgia, and Arkansas.

Correlation analysis, employing the correlation coefficient as a measure of association between two variables, was used to determine the period of the year in

FIG. 21. Relation between the percentage deviation of the annual growth of 8 trees in Carroll County from the trend line and the annual deviation of rainfall from the average during April to June, inclusive, at Eureka Springs. The correlation coefficient for growth and rainfall is + 0.487, and is not statistically significant.
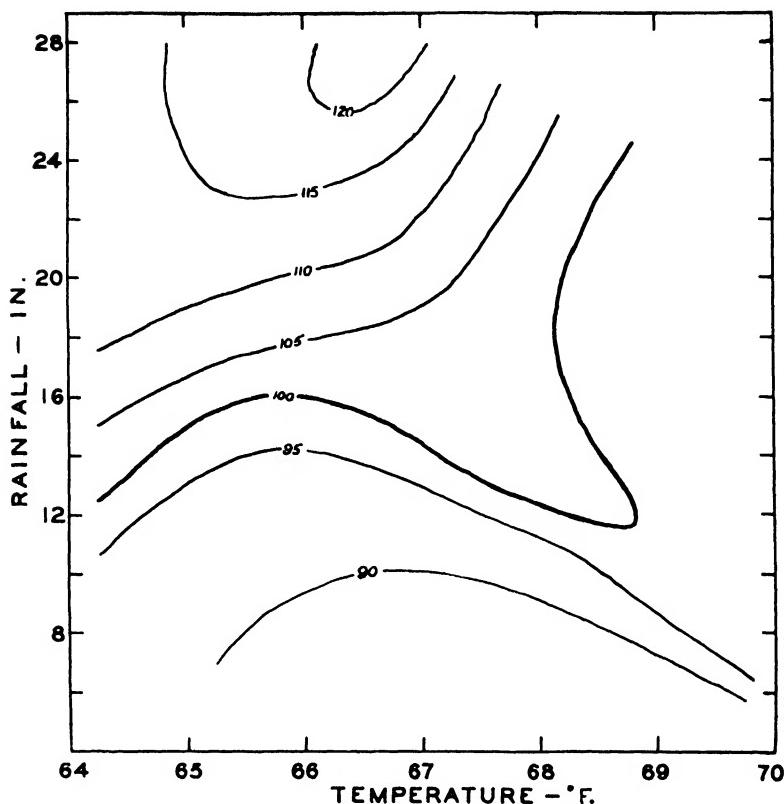
which climatic factors were most influential in determining the annual radial growth. Graphic methods were then employed to illustrate the relationships.

The annual growth of loblolly pine in southwestern Louisiana is influenced most by fluctuations of the total rainfall during January to May, inclusive, the association is positive, that is, increases in rainfall above the mean usually result in an increase in growth under any given conditions of temperature. Less than average rainfall usually results in sub-normal annual growth under any given condition of temperature. Deviations of average temperatures for the same period are negatively correlated with growth. High temperatures are usually associated with low growth and low temperatures are associated with more than average growth.

The annual growth of slash pine and longleaf pine in the Coastal Plain of Georgia is influenced most by rainfall in the early spring—February to April, inclusive. The relationship is positive. The average temperature of the summer period—June to August, inclusive— has the highest negative correlation with growth. High temperatures are associated with low growth.

The temperature of the previous summer is negatively correlated with annual growth, but less strongly than current summer temperatures in the stands studied.

In northern Arkansas, the rainfall for April to June, inclusive, gave the highest positive correlation with the annual growth of shortleaf pine, while the relation of periodic temperature to annual growth exhibits much variation.

Good association was found between annual radial growth and the climatic factors when the trend of radial growth was linear.

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